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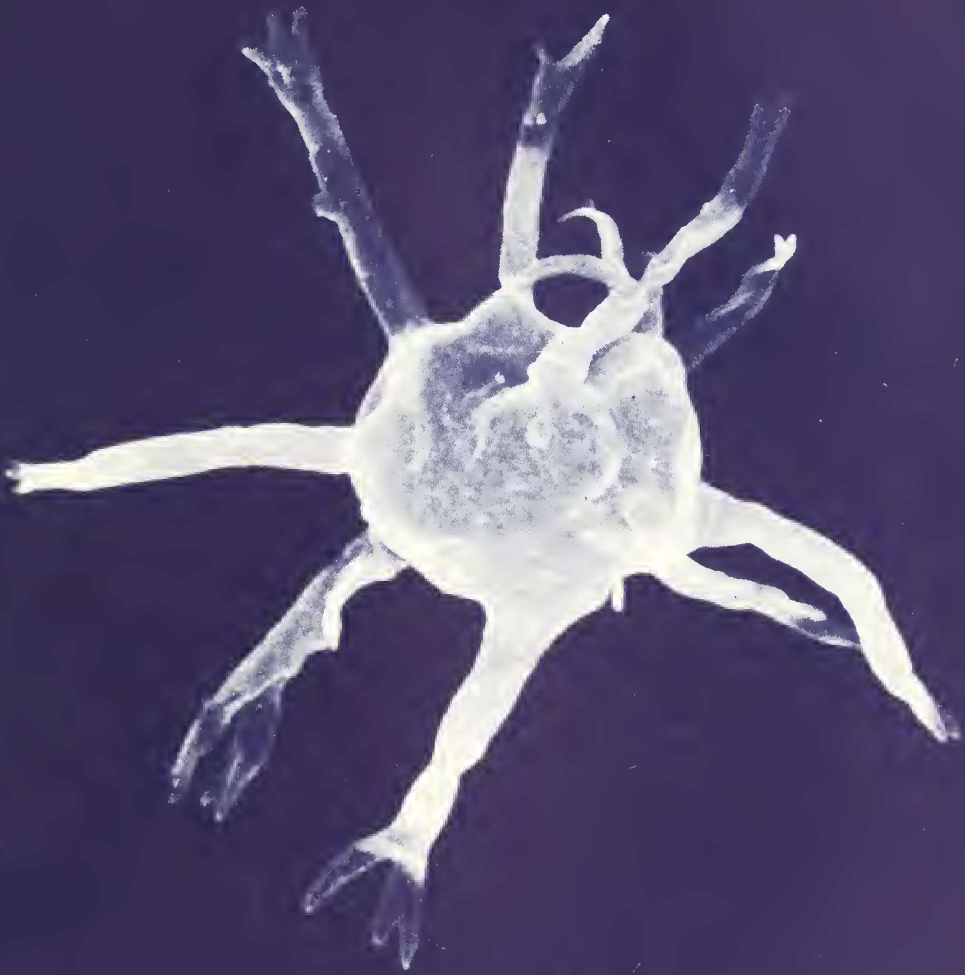

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Cover: An acritarch of the genus *Multiplicisphaeridium* from the Tournaisian Bedford Shale of Ohio, U.S.A. Institute of Geological Sciences specimen number MPK 3569. S.E.M. × 1000. Within the last twenty-five years the number of described acritarch taxa has increased dramatically, and these organisms are now used extensively to date rocks of late Precambrian to Devonian age.

UPPER PROTEROZOIC MICROFOSSILS FROM THE SUMMER ISLES, N.W. SCOTLAND

by ZHANG ZHONGYING

ABSTRACT. A structurally preserved and distinctive microbiota composed of sphaeromorphic acritarchs and filamentous microfossils has recently been recovered from shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles, N.W. Scotland. The dominant sphaeromorphs comprise single vesicles, plurivesicular aggregates, and envelopes containing up to several tens of vesicles. They closely resemble those occurring in shales of the Roper Group, Northern Territory, Australia. Detailed study of the variety of sphaeromorphs has revealed that they probably represent stages in the life cycle of a single species of coccoidal, endospore-forming pleurocapsalean blue-green alga *Torridoniphycus lepidus* gen. et sp. nov. The filaments are hollow tubes ranging from 1·5 up to 53·0 μm wide. They are assigned to the taxa *Eomycetopsis crassiusculum* (Horodyski) comb. nov., *Siphonophycus beltensis* Horodyski, *Siphonophycus* sp., and unnamed larger filaments. Most of them are interpreted as representing discarded sheaths of filamentous oscillatoriacean cyanobacteria, and are similar to those preserved in shales of the lower Belt Supergroup in the Little Belt Mountains, Montana, and the Dismal Lakes Group in Arctic Canada. This microbiota is thought to be of cyanophyte affinity. The low taxonomic diversity and high dominance of a few species may indicate an unusual and restricted aquatic ecosystem.

DURING the last twenty years, most studies of Precambrian life in North America and Australia have centred on microfossils preserved in stromatolitic cherts, which largely represent shallow-water, benthic mat communities (Diver and Peat 1979; Horodyski 1980). Microfossils have also been described from Precambrian shales. Such studies were mainly conducted in the Soviet Union (Timofeev 1966, 1973) and in western Europe (Vidal 1976, 1981). In recent years, however, the study of shale-facies microfossils in Precambrian rocks has increased immensely (Allison and Moorman 1973; Bloeser and Schopf 1977; Cloud, Moorman and Pierce 1975; Diver 1980; Ford and Breed 1973; Hofmann 1977; Hofmann and Aitken 1979; Hofmann, Hill and King 1979; Horodyski 1980; Horodyski, Donaldson and Kerans 1980; Javor and Mountjoy 1976; Knoll and Keller 1979; Knoll, Blick and Awramik 1981; Moorman 1974; Peat *et al.* 1978; Xing Yusheng and Liu Guizhi 1973). These shale-facies microfossils provide the opportunity to study Proterozoic life quite different in appearance from that preserved in stromatolitic chert.

In 1979 P. R. Grant, W. L. Diver, and I made a reconnaissance of the late Proterozoic Aultbea Formation on Tanera Beg, Summer Isles, Highland Region, N.W. Scotland (text-fig. 1). A number of rock samples were collected from grey shales of the Aultbea Formation at different horizons (text-fig. 2). Structurally preserved microfossils, comprising sphaeromorphs and filaments, were found in petrographic thin sections and successfully recovered from macerations (Zhang Zhongying, Diver and Grant 1981). This occurrence prompted further collection of grey shales from some of the other Summer Isles for micropalaeontological investigation. During a return visit in 1980, Grant and Diver collected many samples from other shale horizons at the site of the initial discovery, and their collection was submitted to me for examination. The purpose of the paper is to illustrate, identify, and describe the microfossils from these samples.

GEOLOGICAL SETTING

The Torridon Group of N.W. Scotland consists of some 7 km of unmetamorphosed red beds, with subordinate grey shales (Stewart 1975). The group is separated from overlying Cambrian strata by an angular unconformity, and is itself divisible into four formations from the base upwards: (1) the Diabaig Formation; (2) the Applecross

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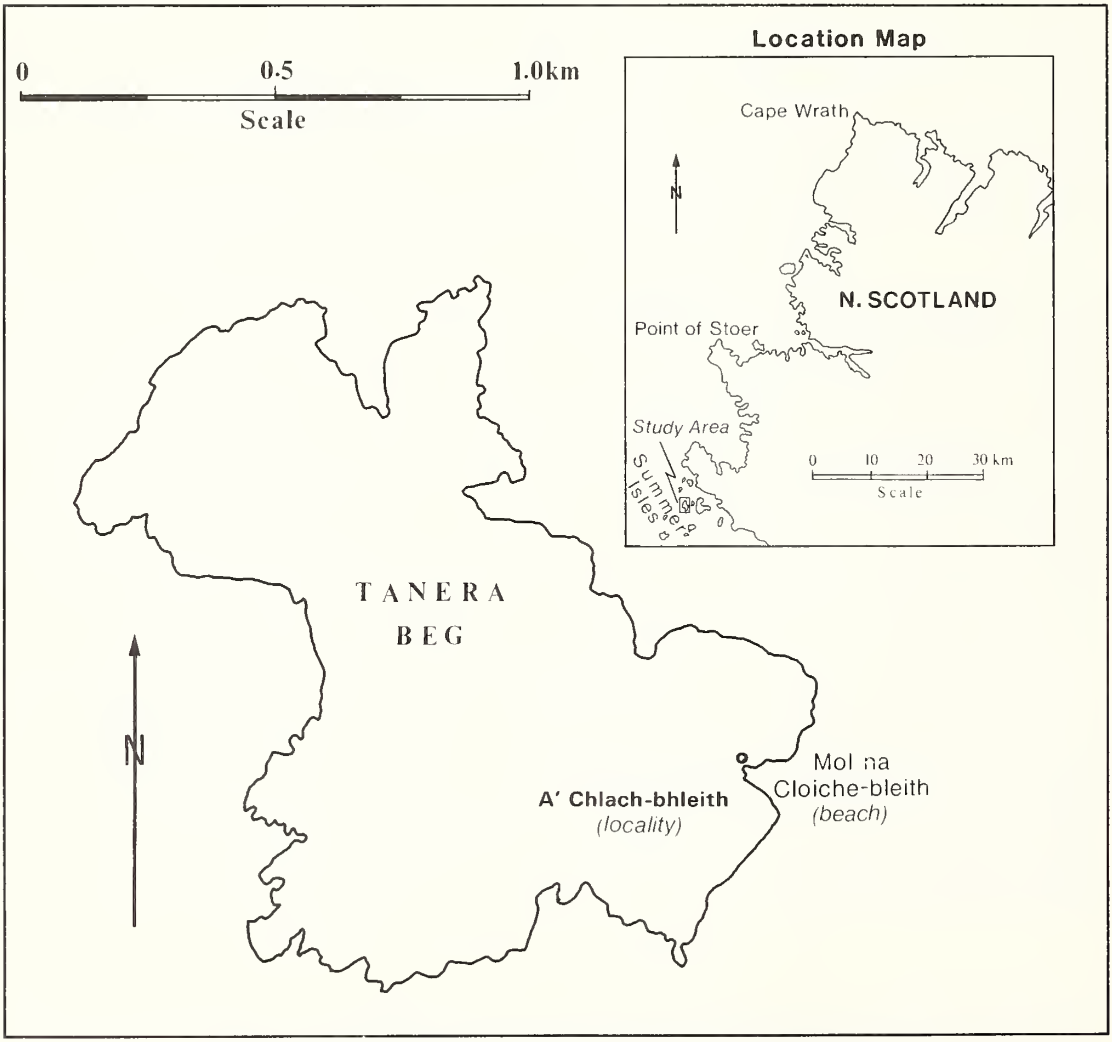
Formation; (3) the Aultbea Formation; (4) the Cailleach Head Formation. Nearly all the grey shales of the group yield abundant microfossils. The underlying Stoer Group, over 2 km thick, also yields microfossils (Downie 1962; Cloud and Germs 1971). According to Downie, the Torridon Group is of upper Riphean age, and the Stoer Group of middle Riphean age (see Stewart 1975). There is a major unconformity between these two groups. Isotopic dating indicates a Rb–Sr whole-rock age of *c.* 777 Ma for the Torridon Group, and *c.* 968 Ma for the Stoer Group (Moorbath 1969; Stewart and Parker 1979) using the decay constant of Steiger and Jäger (1977). Therefore, the unconformity may indicate a long lapse in sedimentation.

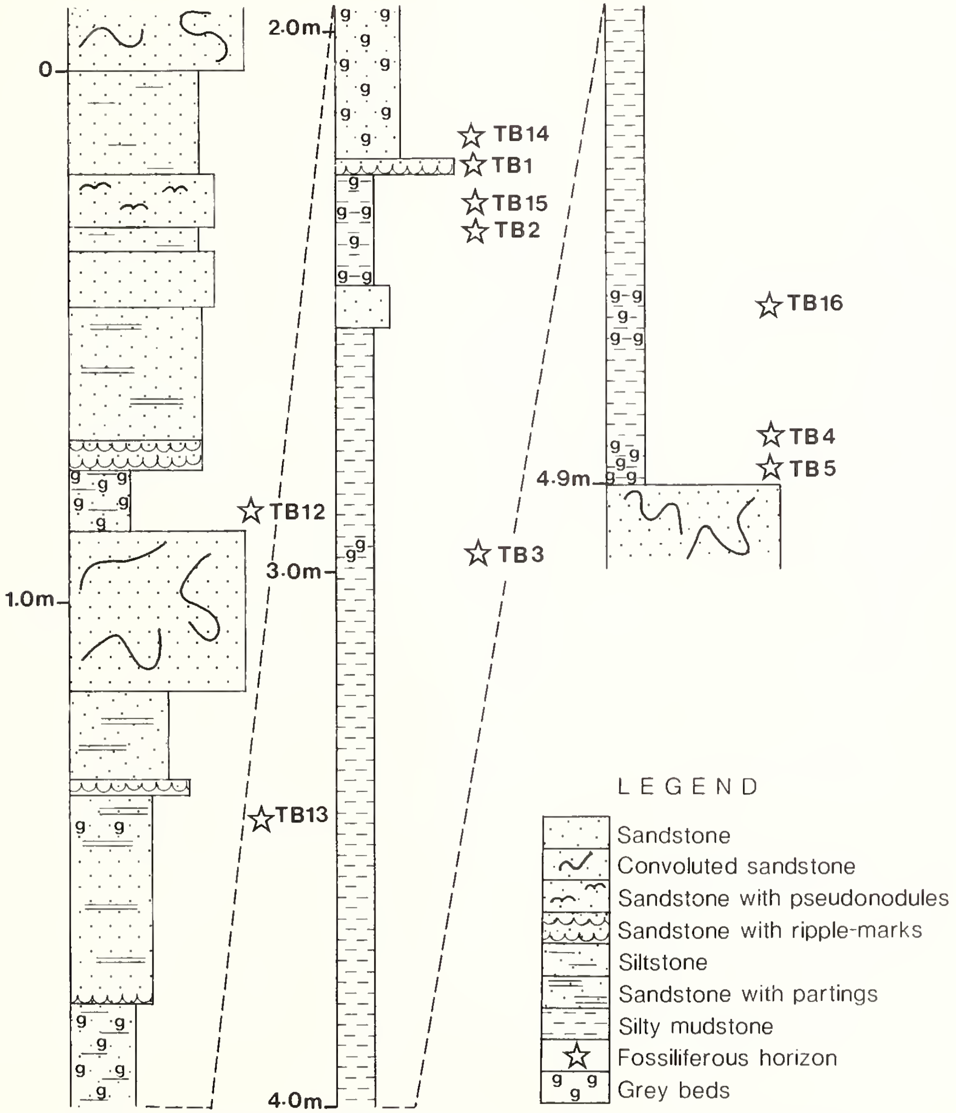
The Torridon Group outcrops extensively on the Summer Isles. Many of these islands and especially the greater part of Tanera Beg are composed of the Aultbea Formation, while the north-west end of Tanera Beg is formed by the Applecross Formation (Gunn 1907). The rock samples came from a grey shale unit in the Aultbea Formation, on the north-east side of A'Chlach-bhleith on the south-east corner of Tanera Beg, Summer Isles (NB 97080722, text-fig. 1). The shale unit, 4·9 m thick, mainly consists of purplish-grey silty mudstone, siltstone and sandstone, intercalated grey shales, and pink arkosic sandstone bands. Although the shale is generally silty, finer-grained intercalations of < 1mm–2 cm also occur. Sixteen rock samples from ten horizons within the shale unit were collected (text-fig. 2). All contained organic walled microfossils, but the best preserved are found in the fine grey shales.



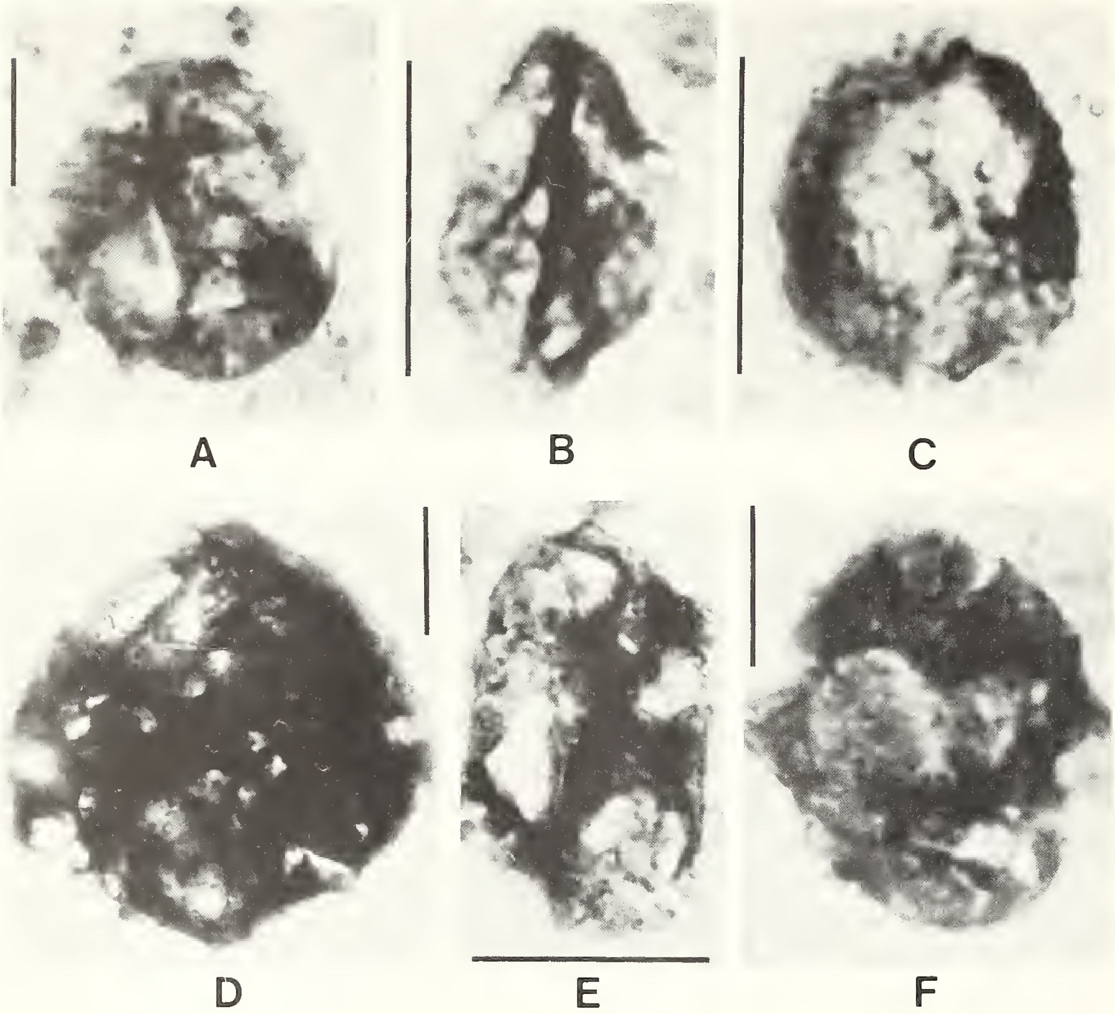
TEXT-FIG. 1. Index map with section location shown with black circle.

PREVIOUS MICROPALAEONTOLOGICAL INVESTIGATIONS

Several reports and descriptions of organic walled microfossils from grey shales of the Torridon Group in N.W. Scotland have been published (Teall 1907; Naumova and Pavlovsky 1961; Downie 1962; Diver 1980). The most detailed study of the Torridonian microbial assemblage has been carried out by W. L. Diver, and has advanced to the point at which relationships between sedimentological controls, palaeoecological factors, and microfossil distribution are being elucidated (Diver 1980; see also Zhang Zhongying *et al.* 1981). However, our knowledge about the fossil record from the Torridon Group of the Summer Isles remains very meagre, even though Gunn (1907) suggested that shale horizons there might contain microfossils.



TEXT-FIG. 2. Fossiliferous grey shale section at Mol na Cloiche-bleith, Tanera Beg. Section measured from the defined top.



TEXT-FIG. 3. Some compressed sphaeromorphic acritarchs (*Torridoniphycus lepidus* gen. et sp. nov.) found in petrographic thin sections cut parallel to lamination. A, TB4-TS502, B8147; B, TB4-TS502, B8148; C, TB3-TS01, B8149; D, TB4-TS502, B8150; E, TB4-TS02, B8151; F, TB4-TS502, B8152. Scale bars in all photographs 10 μm.

METHODS

All rock samples collected were examined in petrographic thin sections and standard palynological macerations. Most petrographic thin sections were cut 30 μm thick, either perpendicular or parallel to lamination. Sometimes thicker thin sections were cut to avoid damaging the fossils. Most of the Tanera Beg fossils are compressed parallel to lamination, and so are readily studied in thin sections cut parallel to lamination (text-fig. 3). In thin sections cut perpendicular to lamination, the microfossils appear only as very thin dark streaks. Most microfossils are difficult to study in thin sections; the organic matter has undergone advanced stages of degradation, and the surrounding clastic sediment and diagenetic mineral crystals obscure and destroy their detailed structure. The microfossils preserved in thin sections of shale samples TB2, TB4, TB12, and TB16 are relatively better preserved and more abundant than the others.

Examination of petrographic thin sections shows that all these microfossils are within the bulk of the shale and are compressed parallel to lamination. These observations indicate that the microfossils are indigenous to the shale and syngenetic with deposition of the surrounding sedimentary matrix. The microfossils lie scattered on the bedding planes of the shale, and their preservation in thin sections is varied. It is likely that most of the microfossils had been carried away or washed around before being deposited with other detritus. The fact that all known filaments lack trichomes and many sphaeromorphs have no internal contents also supports this interpretation. It should be noted, however, that some of them might have been preserved close to their life position, even buried in the sediment during their growth and decay.

Detailed observations on their morphological structure were best carried out in hydrofluoric-acid-resistant residues. Rock samples were cut and the surface ground off on a rotary diamond lap to remove surface contamination and the silty parts of the rock as far as possible. From each sample 30–40 g of rock fragments bordered by fresh surface without obvious fractures were washed with distilled water, and left in 10% HCl until the supernatant was colourless. The HCl treatment usually took a few weeks, sometimes 2–3 months. Then, the fragments were broken down using a mixture of 10% HCl and 40% HF, the proportion of HF being gradually increased until only an organic sludge was left. This took 2–6 months depending on the mineralogy of the rock under investigation. The resulting macerate was washed with distilled water, mounted in glycerine jelly, and then examined in strew-slides under the light microscope. The best microfossils obtained from maceration came from the macerate of shale sample TB5.

Sixty-eight petrographic thin sections and 146 slides of macerates from different horizons in the shale unit on Tanera Beg were examined. Microfossils were measured using a micrometer on an optical microscope, and the dimensions obtained are accurate to within 0·5 μm. Counts were made along random, non-overlapping scan lines.

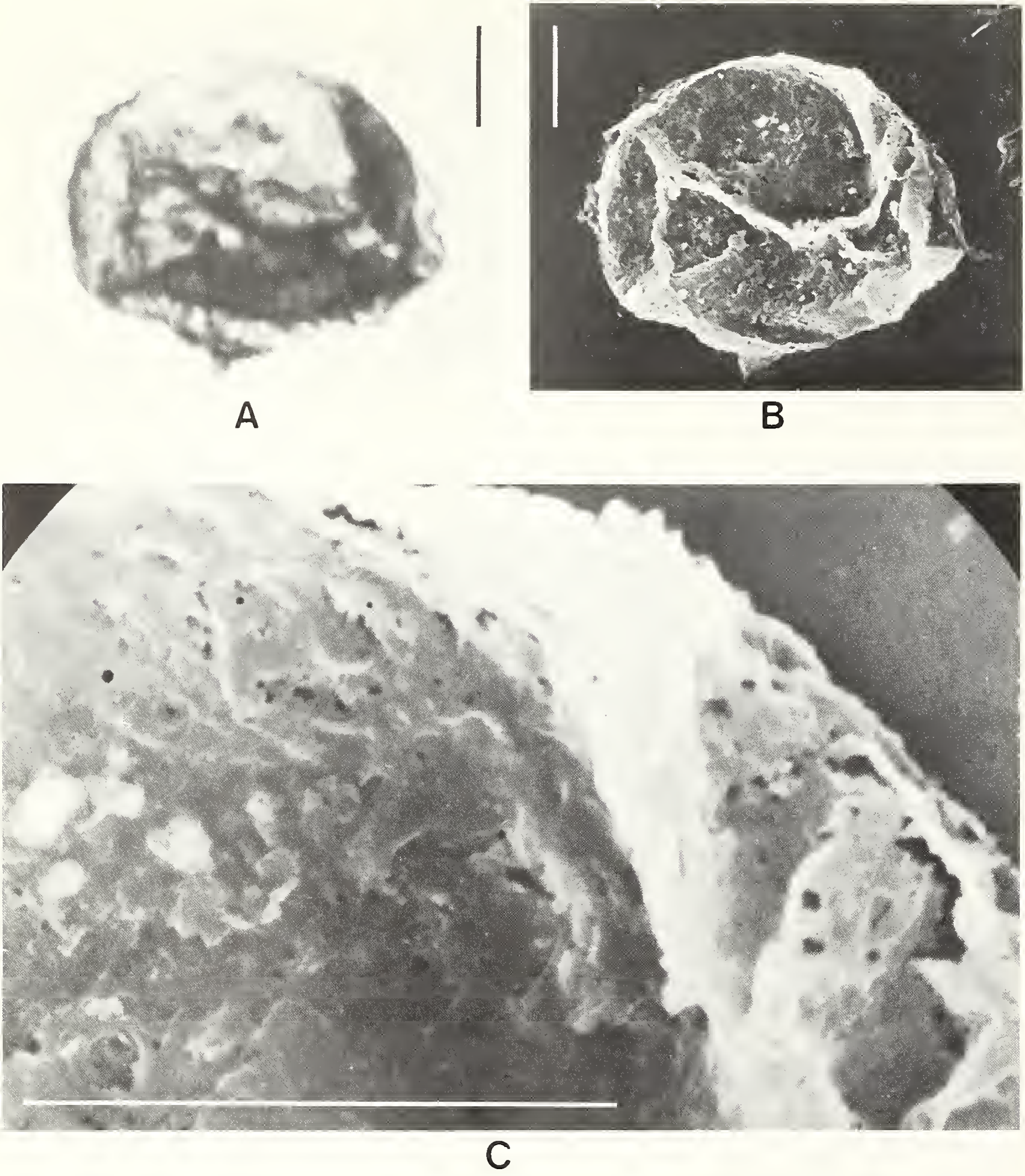
The taxonomic treatment of the Tanera Beg microfossils given below combines observations from petrographic thin sections and macerations. The sphaeromorphs illustrated in this study are mainly described from the macerate of shale sample TB5; it was chosen because it yielded a great variety of sphaeromorphs and the best preserved specimens. Shale sample TB5 also shows a representative and homogeneous fossil assemblage from a narrow stratigraphic interval at the base of the shale unit under study.

Many selected individual microfossils were picked out from the macerate of shale sample TB5 for comparative study by both light microscopy and scanning electron microscopy (text-fig. 4).

PALAEONTOLOGY

As discussed by many palaeontologists (Cloud and Germs 1971; Diver and Peat 1979; Hofmann *et al.* 1979; Loeblich and Tappan 1976; Peat *et al.* 1978; J. M. Schopf 1969; Vidal 1974, 1976), several factors render difficult the systematic study of Precambrian microfossils: (1) Different workers use different taxonomic schemes so that morphologically indistinguishable microfossils are assigned to different taxa. (2) Most specimens have undergone various stages of degradation and diagenesis, and diagnostic surface features have been subjected to modification and obliteration. (3) Invalid names continue to be used in the literature. (4) A great many studies have been conducted in the Soviet Union, but it is difficult to obtain publications and type specimens for study. (5) Comparisons are rendered very difficult by the low quality of the illustrations and the inadequate descriptions of many reports.

The Tanera Beg assemblage consists of two basic types of microfossils, namely the dominant sphaeromorphic acritarchs and the filamentous microfossils. Fossil sphaeromorphs are abundant in the Aultbea grey shales, and a variety of morphologies are evident. Early in the study of these sphaeromorphs, attempts were made to relate them to described material. On this basis they could be assigned to more than a dozen current taxa because of minor differences in preserved morphology, while some of them might be new forms. But this approach seems arbitrary, burdensome, and even unnecessary. An alternative is that most of the sphaeromorphs encountered (but not all) are variants of a single species, which is supported by evidence of continuous variation between morphotypes of the sphaeromorph microfossils, making it difficult to draw a definite line between them. Furthermore, some morphological features are clearly degradationally or preservationally related. Thus, it is reasonable to suppose that many of the Tanera Beg sphaeromorphs represent stages in the life cycle of a single species. Some of them are morphological variants caused by structural

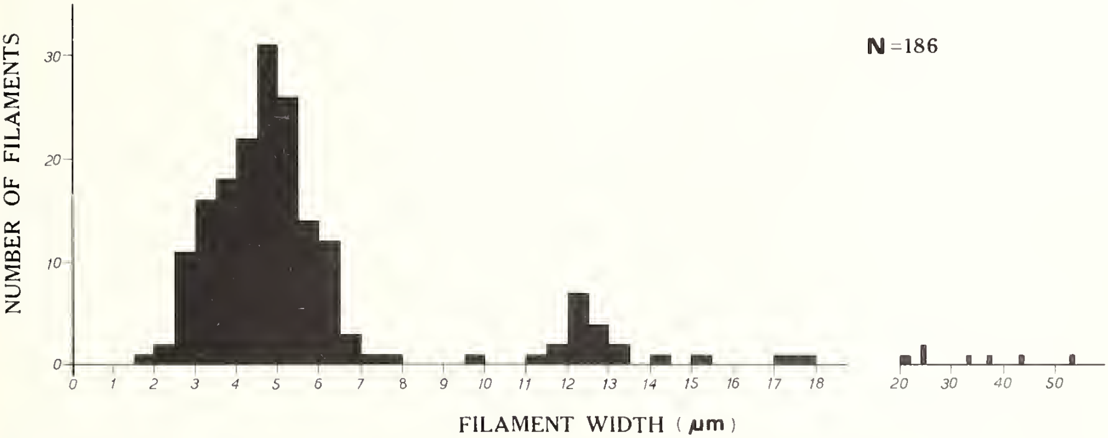


TEXT-FIG. 4. Comparative illustrations of the same single vesicle of *Torridoniphycus lepidus* gen. et sp. nov. in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (from the macerate of shale sample TB5), obtained by light microscopy (Zeiss photomicroscope III) (A, TB5-SEM10, B8153), and scanning electron microscopy (JEOL JSM-35) (B, and C showing detail of the surface of the same specimen). Scale bars in all photographs 10μm.

degradation, compaction, and diagenetic alteration of an organism during fossilization. These post-mortem processes (Awramik, Golubic and Barghoorn 1972; Golubic and Hofmann 1976; Golubic and Barghoorn 1977; Golubic and Campbell 1979; Hofmann 1976; Knoll and Barghoorn 1975; Knoll, Barghoorn and Golubic 1975; Knoll and Golubic 1979) have undoubtedly played an important role in increasing morphological variation.

Comparisons with some modern and fossil endosporulating blue-green algae help in interpreting the Tanera Beg sphaeromorphs. Beck (1963) described in detail the sequence of events in endosporulation of *Pleurocapsa fuliginosa* Hauck, which reproduces by simple binary fission, and by the production of endospores in two slightly different modes (see also Moorman 1974). From his description it is evident that a single species shows a wide size range and a variety of growth forms. Moorman (1974) took Beck's description of *P. fuliginosa* Hauck as a comparative model for interpreting the Hector microbiota from the Canadian Cordillera, and concluded that the microbiota was composed of a single species of endospore-forming blue-green alga described as *Sphaerocongregus variabilis* Moorman. Later Vidal (1976) emended the genus *Bavlinella* Shepeleva and transferred Moorman's species to *Bavlinella faveolata* (Shepeleva). It seems that this transfer is not warranted by present evidence and the two taxa are treated separately here. Knoll *et al.* (1981) followed Moorman (1974) in interpreting most of the microfossils in the Mineral Fork Formation, Utah, as stages in the life cycle of a single taxon, *B. faveolata* (Shepeleva) Vidal. Waterbury and Stanier (1978) described patterns of growth and development in pleurocapsalean cyanobacteria which support Moorman's interpretation; they placed in the Pleurocapsales all cyanobacteria which reproduce by the liberation of endospores formed through multiple fission. All of these important researches encouraged me to elaborate the diverse morphologies of the Tanera Beg sphaeromorphs and include most of them in a single species rather than to divide them arbitrarily into separate taxa.

The Tanera Beg filaments are most similar to those preserved in shales of the lower Belt Supergroup in the Little Belt Mountains, Montana (Horodyski 1980), and the Dismal Lakes Group in Arctic Canada (Horodyski *et al.* 1980). All preserved filamentous forms are apparently unbranched, originally tubular structures that were compressed during compaction of the surrounding clastic sediment. They range from 1·5 to over 50·0 μm wide, and lack cross walls or other evidence of cellular organization. In petrographic thin sections, they are brown to black in colour, and occur as both isolated filaments and fragments of filament aggregations. In some thin sections (shale sample TB4) cut parallel to lamination, their abundance reaches 41 filaments/cm^2. Measurements of 186 filaments in 15 sections reveal a bimodal size distribution (text-fig. 5). Filaments 1·5–8·0 μm wide comprise the



TEXT-FIG. 5. Size distribution of filamentous microfossils in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (186 filaments measured in 15 petrographic thin sections cut parallel to lamination).

primary mode of the distribution. Assuming an initially cylindrical shape, undeformed specimens in the Aultbea assemblage would be 1–5 μm in diameter (= compressed width × 2/π). Filaments less than 2·5 μm wide might be assigned to *Archaeotrichion* Schopf (1968). They are not formally described in this paper because of their rare occurrence. Filaments 2·5–8·0 μm wide are here referred to *Eomycetopsis* Schopf (1968). The secondary mode is a rather small one, and its size range (11·0–13·5 μm in width) lies reasonably within a single taxon (*Siphonophycus beltensis* Horodyski). Larger filaments up to 53 μm wide are also present, but they are not common. Most of the Tanera Beg filaments are here interpreted as representing discarded sheaths of oscillatoriacean cyanophytes.

All specimens illustrated in this paper are deposited in the Geology Department Type-Fossil Collection, Nanjing University, Nanjing, China, under catalogue Palaeobot. Coll., Nanjing Univ. B8111–8153. Rock samples and the macerate of shale sample TB5 are also housed at the British Museum (Natural History), London.

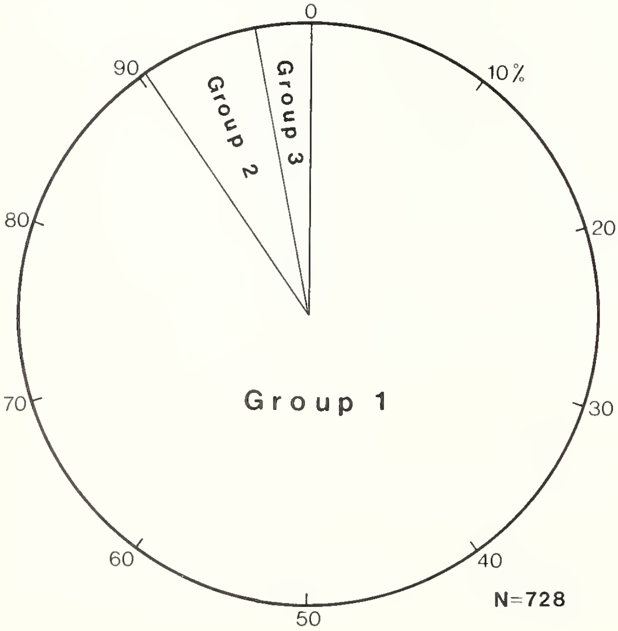
Division CYANOBACTERIA
Class COCOGONEAE
Order PLEUROCAPSALES
Genus TORRIDONIPHYCUS gen. nov.

Type species. Torridoniphycus lepidus sp. nov.

Derivation of name. From the Torridon Group.

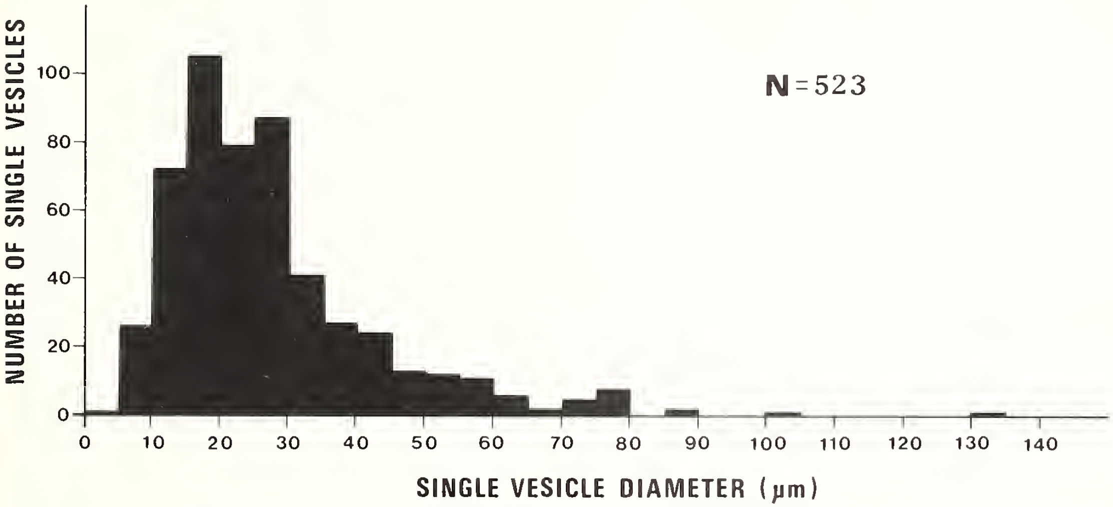
Diagnosis. The genus is composed of three distinctive morphological groups: (1) single vesicles; (2) plurivesicular aggregates; (3) envelopes containing many to several tens of vesicles. The first morphological group is the most abundant (text-fig. 6).

(1) Single vesicles, circular to elliptical, single-walled, light brown to black (Pl. 46, figs. 1–14; text-figs. 3, 4). They range in size from 4 to 125 μm in diameter, but most fall within the range 10–25 μm (text-fig. 7). Preserved surface texture chagrenate, psilate, granulate, scabrous, spongy, or microrugulose, often with various wrinkles and folds, or irregularly shaped mineral grain impressions or perforations. Many of the larger vesicles open by median splits. The original surface is



TEXT-FIG. 6. Relative proportions of three morphological groups (Group 1—90·4%, Group 2—6·5%, Group 3—3·1%) of *Torridoniphycus lepidus* gen. et sp. nov. in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (728 specimens counted in 42 slides from the macerate of shale sample TB5).

thought to be smooth to finely granulate; other surface textures and ornamented wrinkles and folds are probably preservational features resulting from degradation and post-sedimentary compaction. Small vesicles represented by those in text-fig. 3B, C, E, and Pl. 46, figs. 1, 6, 4–22 μm in diameter, are interpreted as spores or 'baeocytes' (Waterbury and Stanier 1978) released by endosporangia, or as 'nannocytes' (Fritsch 1945; Geitler 1960). Some of them might also represent stages in cell growth. The specimen in Pl. 46, fig. 11 shows a cell undergoing the degradation process. Its outer layer is interpreted as a sheath originally enclosing the cell, while the inner dark body represents coalesced and degraded remnants of the entire cell. Such specimens as those shown in Pl. 46, figs. 9, 12, 13 are taken as empty sheaths indicating the final products of the degradation process of independent cells, or endosporangial walls (Pl. 46, figs. 8, 10). It should be noted that larger vesicles in excess of 100 μm in diameter have been encountered, but these are exceedingly rare.



TEXT-FIG. 7. Size distribution of single vesicles of *Torridoniphycus lepidus* gen. et sp. nov. in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (523 single vesicles measured in 61 slides from the macerate of shale sample TB5).

(2) Plurivesicular aggregates, from 20 up to more than 100 μm across, consist of 4, 8, 16, and up to several hundreds of rounded vesicles. These aggregates (Pl. 46, figs. 15–18, 20, 22) are interpreted as representing the successive products of binary fission. Their outer gelatinous envelopes, if present, might be broken up during cell division. Cell division seems to be binary only. The individual vesicles, single-walled, 10·0–17·5 μm in diameter, are closely packed to form globose masses. Vesicles are diagenetically modified; the original surface is thought to be smooth to finely granulate. Inner dark bodies can also occur in some vesicles.

(3) Envelopes containing vesicles. This morphological group (Pl. 46, figs. 19, 21, 23, 24) is taken as representing events of ordinary endospore formation through multiple fission. The specimen in Pl. 46, fig. 21 is interpreted as an endosporangium, and those in Pl. 46, figs. 19, 23, 24 as incomplete endosporangia or their broken pieces with attached endospores. Endosporangia, 35–> 100 μm across, clearly contain up to several tens of spores. Endospores, spheroidal, 4–22 μm in diameter, are loosely or closely distributed within a common non-lamellar organic envelope. The envelope opens by median splits, and occasionally splits up into several sheets or ribbons with endospores still attached. The specimen in Pl. 46, fig. 8 shows a nearly empty endosporangial wall (group 1) and three spores being released from one end.

Discussion. Although this taxon closely resembles *Sphaerocongregus* Moorman in the morphologically variable growth forms, there are some important differences which justify a new genus: (1) *Sphaerocongregus* forms linear aggregates which are unknown in *Torridoniphycus.* (2) *Torridoniphycus* forms tetrads which have not been reported in *Sphaerocongregus.* (3) The outer envelopes of *Torridoniphycus* open by median splits which have not been seen in *Sphaerocongregus.* (4) Comparable individuals of *Sphaerocongregus* are much smaller in size than those of *Torridoniphycus.* However, the intermediate growth forms of the latter are more complete and abundant than the former.

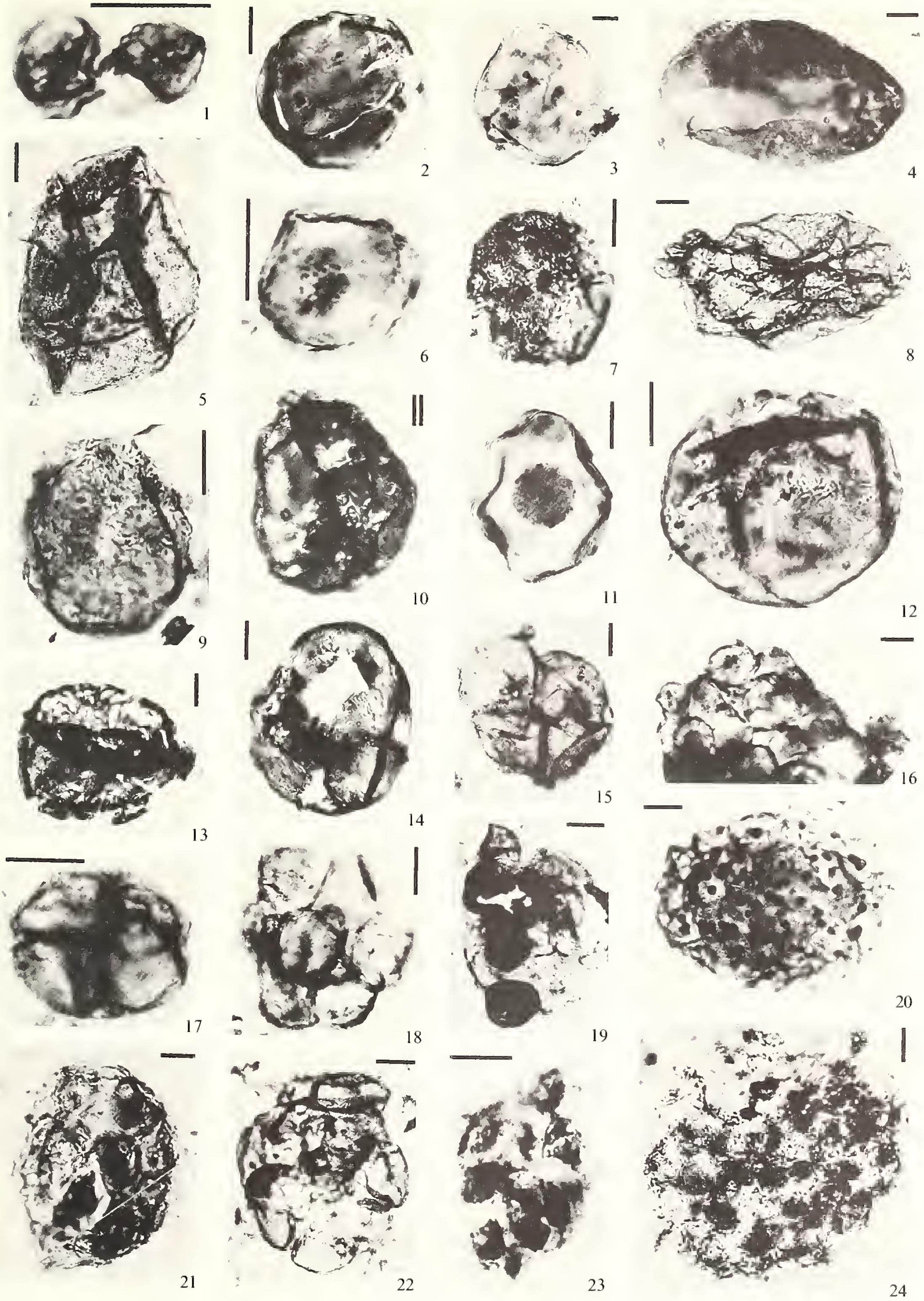
In her paper, Moorman (1974) referred *S. variabilis* to endospore-forming blue-green algae, but its exact taxonomic position was left in doubt. Later Cloud *et al.* (1975) concluded that *S. variabilis* was related to living entophysalidaceans, and had affinities with both the chroococcalean and chamaesiphonalean cyanophytes. According to Knoll *et al.* (1981), the closer analogues to the Hector microbiota seem to be the genera *Xenococcus* and *Dermocarpa*, the latter having also been placed in the order Pleurocapsales by Waterbury and Stanier (1978).

I prefer to assign *Torridoniphycus* to the endosporangiate blue-green algae and more particularly to the order Pleurocapsales, but the possibility of affinities with higher algae, and especially Chlorophyta, still remains. In fact, endospore formation in the blue-green algae is very similar morphologically to aplanospore formation among the green algae (Cloud *et al.* 1975). Similarly, the Tanera Beg sphaeromorphs can also be classified in other ways. But a final solution is impossible without more comparable living analogues.

EXPLANATION OF PLATE 46

Structurally preserved sphaeromorphic acritarchs in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles, Highland Region, N.W. Scotland. All specimens are acid-resistant residues obtained by hydrofluoric acid maceration from shale sample TB5. Photographs in figs. 3, 4, 8, 10, 16, 21, 24 were obtained using transmitted-light, dry-objective optics; all others using transmitted-light, oil-immersion optics. Figure 21 is a composite photograph. Single bar scale is 10 μm long; double bar scale 20 μm long. Slide number and the Paleobot. Coll. Nanjing Univ. number are given for each specimen. All specimens appear to represent possibly different developmental stages of a single taxon, *Torridoniphycus lepidus* gen. et sp. nov., interpreted as an endospore-forming pleurocapsalean blue-green alga.

Figs. 1–24. *Torridoniphycus lepidus* gen. et sp. nov., composed of single vesicles (figs. 1–14), plurivesicular aggregates (figs. 15–18, 20, 22), and envelopes containing many to several tens of vesicles (figs. 19, 21, 23, 24). 1, small vesicles (spores), TB5-MAC26, B8111. 2, chagrenate surface with narrow peripheral wrinkles, TB5-MAC44, B8112. 3, psilate to slightly granular surface, TB5-MAC15, B8113. 4, elliptical vesicle with scabrous or microrugose surface texture opens by a wide median split, TB5-MAC38, B8114. 5, vesicle with wrinkles and folds, TB5-MAC61, B8115. 6, vesicle with a more or less diffuse, granular inner body, TB5-MAC60, B8116. 7, scabrous to spongy surface texture, TB5-MAC32, B8117. 8, vesicle interpreted as a nearly empty endosporangial wall with three spores being released from one end, TB5-MAC25, B8118. 9, vesicle surface covered with very fine microfolds, TB5-MAC04, B8119. 10, large vesicle (endosporangial wall) having small and large perforations, TB5-MAC46, B8120. 11, vesicle containing a large granular inner body, TB5-MAC05, B8121. 12, vesicle surface with a few narrow folds and very fine microfolds, TB5-MAC53, B8122. 13, vesicle surface with irregularly shaped mineral grain impressions or perforations, TB5-MAC29, B8123. 14, vesicle surface with irregularly shaped openings, TB5-MAC28, B8124. 15, tetrad, TB5-MAC05, B8125. 16, plurivesicular aggregate consisting of tens of vesicles tightly compressed together, TB5-MAC01, B8126. 17, tetrad, TB5-MAC13, B8127. 18, plurivesicular aggregate (possibly 8), TB5-MAC46, B8128. 19, ribbon of vesicles, interpreted as a broken piece of endosporangium on which endospores are still attached, TB5-MAC32, B8129. 20, plurivesicular aggregate consisting of about a hundred vesicles, TB5-MAC05, B8130. 21, a well-defined envelope containing vesicles, interpreted as an endosporangium containing endospores, holotype, TB5-MAC29, B8131. 22, plurivesicular aggregate (possibly 16), TB5-MAC59, B8132. 23, vesicles (attached endospores) within a broken envelope (endosporangium), TB5-MAC26, B8133. 24, large sheet of vesicles, interpreted as a large piece of endosporangium on which endospores are still attached, TB5-MAC32, B8134.



ZHANG ZHONGYING, Precambrian sphaeromorph microfossils

It should be noted that among the diverse Tanera Beg sphaeromorphs it is difficult to distinguish between larger spores and smaller cells, between single enlarged cells in the final stage of degradation and endosporangial walls, and between ordinary endosporangia and those of the binary fission type if the latter are covered with an outer gelatinous envelope. However, it seems that ordinary endospore formation might be a fairly simultaneous process, different from the successive process of binary fission or 'nannocyte-formation' as described by Geitler (1925, 1960).

The genus *Torridoniphycus* is based on a series of well-preserved specimens representing various stages of the life cycle and occurring in the same horizon. A speculative reconstruction of the life cycle for the Tanera Beg sphaeromorphs (*Torridoniphycus lepidus* gen. et sp. nov.) is illustrated in text-fig. 8.

Torridoniphycus lepidus sp. nov.

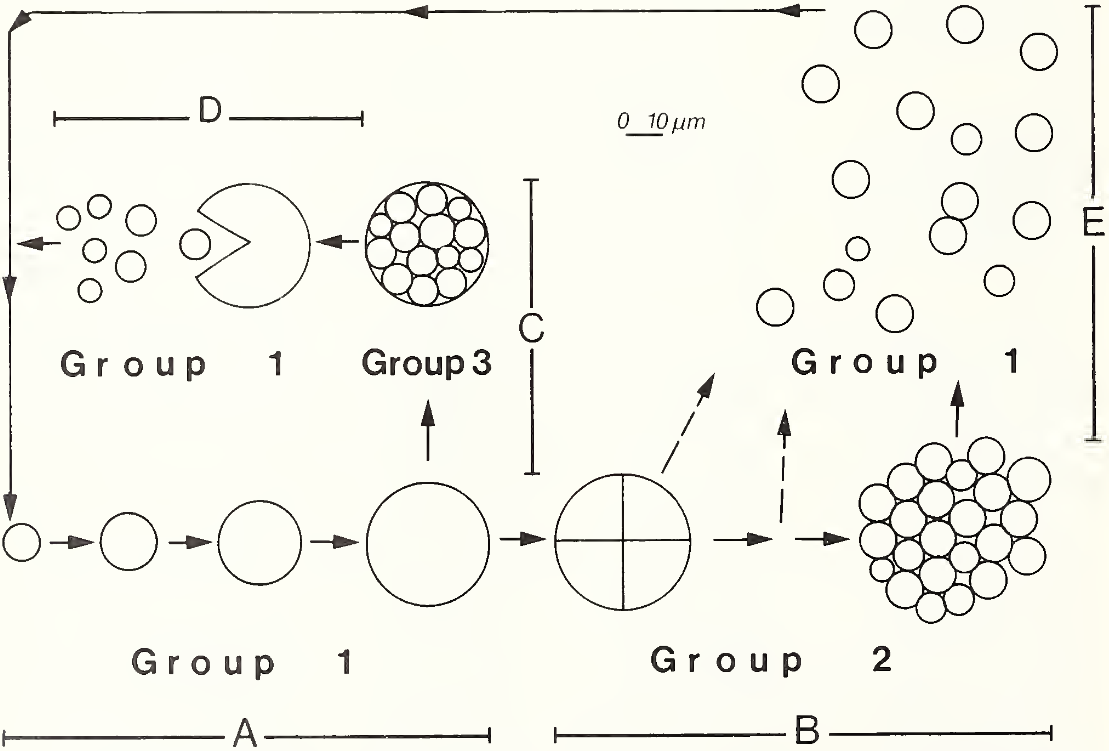
Plate 46, figs. 1-24; text-figs. 3, 4, 6, 7, 8

Type specimens. The fossil in Pl. 46, fig. 21 is cited as holotype (TB5-MAC29, B8131). All other specimens illustrated are paratypes.

Origin of name. After the delicate appearance of the type specimens.

Type locality and horizon. Shale sample TB5, near the base of a grey shale unit in the Aultbea formation, Torridon Group, on the north-east side of A'Chlach-bhleith on the south-east corner of Tanera Beg, Summer Isles, Highland Region, N.W. Scotland (NB 97080722).

Diagnosis. As for genus.



TEXT-FIG. 8. Hypothetical life cycle for *Torridoniphycus lepidus* gen. et sp. nov.: A, cell growth; B, repeated binary fissions; C, endospore formation through multiple fission; D, endospore (baeocyte) release; E, 'nannocyte' release.

Class HORMOGONEAE
Order OSCILLATORIALES
Genus EOMYCETOPSIS Schopf, 1968 emend. Knoll and Golubic, 1979

Type species. Eomycetopsis robusta Schopf, 1968, p. 684, pl. 82, figs. 2, 3; pl. 83, figs. 1–4.

Eomycetopsis crassiusculum (Horodyski, 1980) comb. nov.

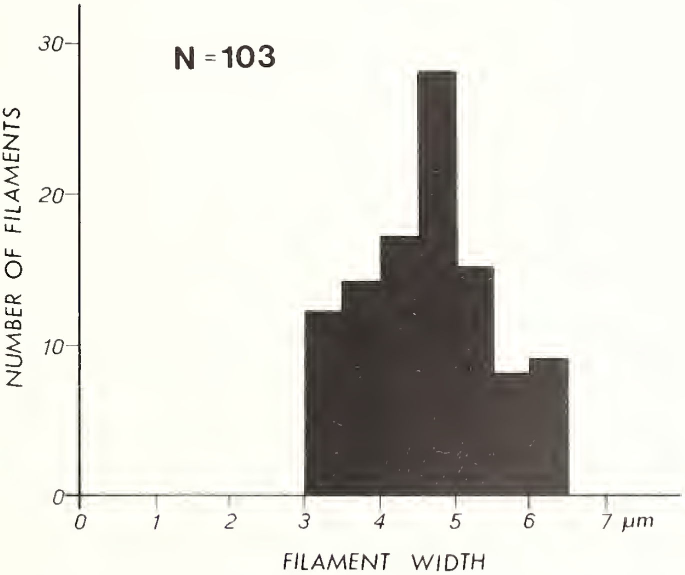
Plate 47, figs. 3–6, 9–13; text-fig. 9

1980 *Siphonophycus crassiusculum* Horodyski, p. 656, pl. 1, figs. 6, 7.
1980 *Siphonophycus crassiusculum in* Horodyski, Donaldson and Kerans, p. 1166, fig. 3*b*–*e*.

Description. Filaments uniform, flattened, non-septate, unbranched, generally gently curved, occasionally flexed or twisted, up to 900 μm long, 3·0–6·5 μm across, width averaging 4·6 μm (103 filaments measured); solitary, or irregularly clustered. Walls less than 0·5 μm thick, dark brown to black; surface texture psilate to granulate.

Discussion. Eomycetopsis Schopf (1968) was originally thought to be marked by occasional septa. Re-examining the type specimens of this taxon, Hofmann (1976) found the supposed 'septa' to be folds or inflections in the wall of non-septate tube. Based on the discovery of cellular remnants and the recognition of the mat-like arrangement of tubule populations, Knoll and Golubic (1979) corroborated the suggestion of Hofmann, and formally emended the genus.

These filaments may represent flattened sheaths of oscillatoriacean cyanophytes closely resembling *Siphonophycus crassiusculum* Horodyski from the lower Belt Supergroup (Horodyski 1980) and the Dismal Lakes Group (Horodyski *et al.* 1980). Removing the effects of flattening (2 × width/π), the diameters of the *S. crassiusculum* tubes would be 1·9–4·2 μm across, which falls within the size range given for *Eomycetopsis* Schopf (1968). Thus, Horodyski's species (3–7 μm wide) is here transferred to the genus *Eomycetopsis*. It is possible that *Eomycetopsis crassiusculum* (Horodyski) is a synonym of



TEXT-FIG. 9. Size distribution of *Eomycetopsis crassiusculum* (Horodyski) comb. nov. filaments in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (103 filaments measured in 11 petrographic thin sections cut parallel to lamination).

E. robusta Schopf and/or *E. filiformis* Schopf from the Bitter Springs stromatolitic cherts (Schopf 1968). Since there is no good basis to prove these to be conspecific, however, the continued use of these names will serve a useful purpose if each is restricted to the lithofacies from which it was originally described.

E. crassiusculum (Horodyski) is the most common filament in the shale of the Aultbea Formation of the Summer Isles.

Genus SIPHONOPHYCUS Schopf, 1968

Siphonophycus beltensis Horodyski, 1980

Plate 47, figs. 1, 2

Description. Filaments broad, compressed, non-septate, unbranched, generally gently curved, solitary, up to 250 μm long, 11·0–13·5 μm across, with wall less than 0·2 μm thick. Surface texture psilate, with irregular transverse markings.

Discussion. These filaments have the morphological characteristics of *Siphonophycus beltensis* Horodyski from the lower Belt Supergroup (Horodyski 1980) and the Dismal Lakes Group (Horodyski *et al.* 1980). These flattened tubes are best interpreted as preserved sheaths of oscillatoriacean algae, but all known specimens lack preserved trichomal contents.

Siphonophycus sp.

Plate 47, fig. 7

Description. Flattened fragments of simple, non-septate, unbranched filaments, 9·5–25·0 μm wide. Surface diagenetically modified, psilate to irregularly granulated; feint transverse markings in some places.

Discussion. These filaments probably represent the preserved empty sheaths of oscillatoriacean algae.

Unnamed Larger Filaments

Plate 47, fig. 8

Discussion. Filaments larger than 25 μm wide are rare in the Aultbea Formation of the Summer Isles. The largest fragment measured is 53 μm wide. These specimens resemble sheaths of extant *Lyngbya*-like oscillatoriacean cyanophytes.

EXPLANATION OF PLATE 47

Structurally preserved filamentous microfossils in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles, Highland Region, N.W. Scotland. Specimens shown in figs. 2, 3, 6, 7, 8, 13 are acid-resistant residues obtained by hydrofluoric acid maceration; all others are in petrographic thin sections cut parallel to lamination. Photographs in figs. 3, 4, 5, 11, 12 were obtained using transmitted-light, oil-immersion optics; all others using transmitted-light, dry-objective optics. Figures 12 and 13 show composite photographs. Single bar scale is 10 μm long; double bar scale 20 μm long. Thin section (or slide) number and the Paleobot. Coll. Nanjing Univ. number are given for each specimen. All specimens appear to represent discarded sheaths of oscillatoriacean cyanophytes.

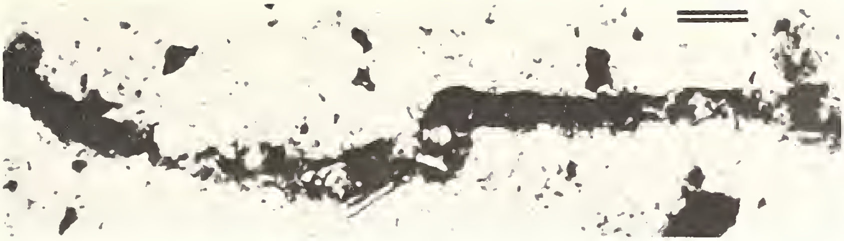
Figs. 1, 2. *Siphonophycus beltensis* Horodyski. 1, TB4-TS506, B8135. 2, TB5-MAC10, B8136.

Figs. 3–6, 9–13. *Eomycetopsis crassiusculum* (Horodyski) comb. nov. 3, TB5-MAC16, B8137. 4, TB4-TS502, B8138. 5,TB2-TS101, B8139. 6, TB5-MAC06, B8140. 9, TB2-TS101, B8141. 10, TB4-TS503, B8142. 11, part of the specimen in fig. 10. 12, TB4-TS504, B8143. 13, TB5-MAC06, B8144.

Fig. 7. *Siphonophycus* sp., TB5-MAC08, B8145.

Fig. 8. Unnamed larger filament, TB5-MAC16, B8146.

PLATE 47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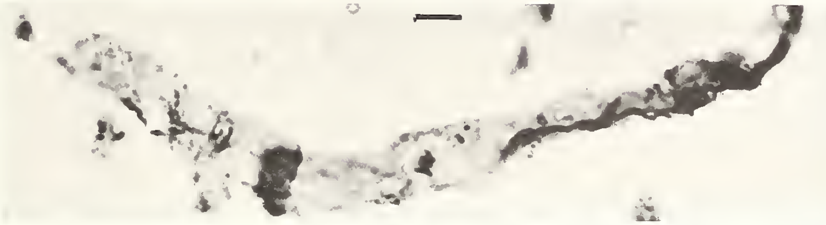
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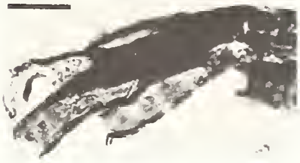
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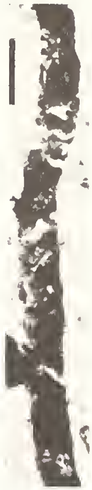
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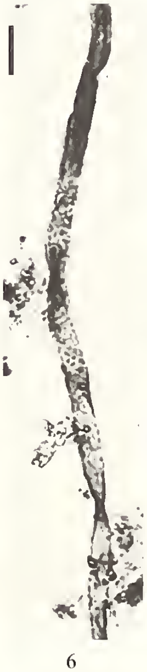
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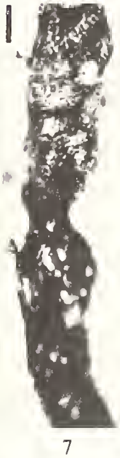
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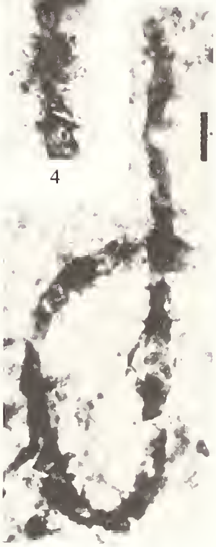
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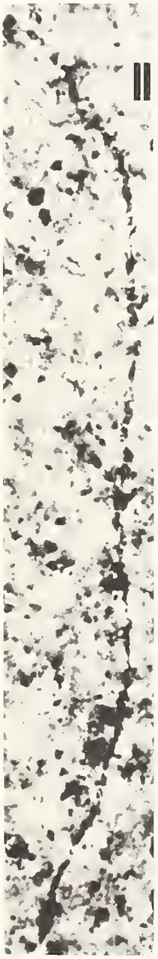
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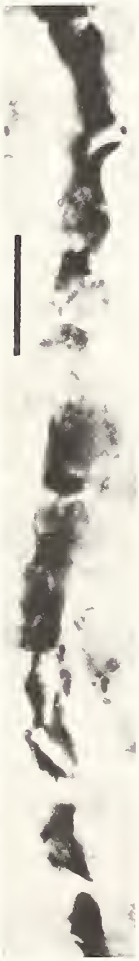
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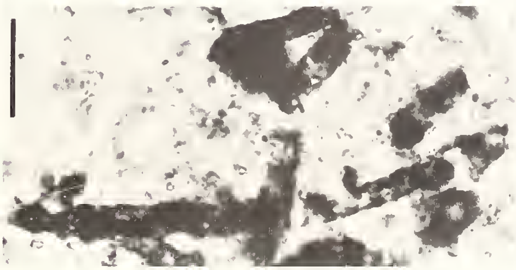
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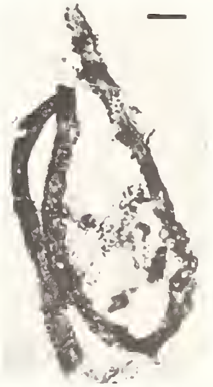
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ZHANG ZHONGYING, Precambrian filamentous microfossils

DISCUSSION AND SUMMARY

The *c.* 800 Ma old Tanera Beg microbiota is composed of two basic types of microfossils, namely the dominant sphaeromorphs and the filaments. Although the sphaeromorphs show a variety of morphologies, this microbiota is of low taxonomic diversity. The sphaeromorphs are completely dominated by various growth forms of a single taxon, *Torridoniphycus lepidus* gen. et sp. nov., which is thought to be an endospore-forming pleurocapsalean blue-green alga, which might have grown as epiliths on rocks. Most of the filaments are interpreted as representing discarded sheaths of oscillatoriacean cyanobacteria, and might have beeen planktonic. Thus, the Tanera Beg microbiota is most likely of cyanophyte affinity.

The sandstone of the Torridon Group is generally thought to be of fluvial origin, but much debate has centred on the depositional environment of the grey shales in the group. Some geologists considered that the environment was tidal (Peach *et al.* 1907, p. 325), tidal marine (Allen *et al.* 1960), and marine (Stewart 1969), while others described it as fresh water, such as lacustrine (Selley 1965*a*, *b*). By using a refined version of the boron palaeosalinity indicator, Stewart and Parker (1979) concluded that the grey shales in the Stoer and Torridon groups are non-marine. As modern pleurocapsalean algae have a wide natural distribution, occurring in terrestrial, freshwater, and marine environments (Golubic 1976; Waterbury and Stanier 1978), the occurrence of the Tanera Beg sphaeromorphs and filaments cannot give any particular interpretation strong support. However, the salinity of the water is uncertain. The low taxonomic diversity and the high dominance a few species of the microbiota may indicate an unusual and restricted aquatic ecosystem, such as a marine embayment or a lake.

Some sphaeromorphs of the Tanera Beg assemblage are similar to those described from Middle and Upper Proterozoic shales in the Soviet Union (Timofeev 1966, 1973), Sweden (Vidal 1974, 1976, 1981), Australia (Peat *et al.* 1978), Canada (Hofmann and Aitken 1979; Horodyski *et al.* 1980), and the United States (Horodyski 1980). Among these microbiotas, the Tanera Beg sphaeromorphs closely resemble, on the whole, those occurring in the *c.* 1300–1400 Ma shales of the Roper Group, Northern Territory, Australia (Peat *et al.* 1978). It appears that many sphaeromorphic forms of the Roper microbiota might also be interpreted as representing stages in the life cycle of a *Torridoniphycus*-like alga. As far as the Tanera Beg filaments are concerned, they are remarkably similar to those preserved in shales of the *c.* 1400 Ma lower Belt Supergroup in the Little Belt Mountains, Montana, and the *c.* 1200 Ma Dismal Lakes Group in Arctic Canada. As mentioned above, the Torridon Group has been dated at *c.* 800 Ma. If these isotopic age data are correct, the similarities between these microbiotas probably reflect the widespread occurrence of oscillatoriacean cyanophytes and *Torridoniphycus*-like algae during Middle and Late Proterozoic time.

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OSTEOLOGY OF THE JURASSIC LIZARD *ARDEOSAURUS BREVIPES* (MEYER)

by NIALL J. MATEER

ABSTRACT. A description is given of a new and well-preserved specimen of *Ardeosaurus brevipes* from the Solnhofen facies of the Kimmeridgian of Bavaria, Germany. The specimen is in the Paleontological Museum of Uppsala University (PMU.R58). The type of *A. brevipes* is missing and only a cast represents the poorly preserved original. The new specimen has characters exemplifying the similarities between the two species of *Ardeosaurus*: *A. brevipes* and *A. digitatellus*. Differences between *Ardeosaurus* and a similar genus *Eichstaettisaurus* are clarified and emphasized. The specimen is compared with other Jurassic lizards also probably belonging to the Gekkota: *Yabeinosaurus*, *Bavarisaurus*, and *Palaeolacerta*.

A NEW specimen of the Jurassic lizard *A. brevipes* was recently discovered in the collections of the Paleontological Museum in Uppsala, previously having been labelled as *Homeosaurus*. The genus *Ardeosaurus* is known only from the Kimmeridgian of Germany, and the present specimen is from Solnhofen. Nothing is known of the purchase or collection of this specimen by the museum.

Three other specimens represent this genus, one of which, the type for *Ardeosaurus*, is apparently lost and is represented only by a cast. The other two specimens, both from Solnhofen, have been referred to the species *A. digitatellus* (Cocude-Michel 1963) and *A.* cf. *digitatellus* (Grier 1914). All three of these specimens are poorly preserved and do not reveal much osteological detail. However, a closely related genus, *Eichstaettisaurus* from Eichstätt, is well-preserved and provides a useful comparison with the present specimen. A review of the taxonomic history of this genus is given by Hoffstetter (1964) and of its present status by Estes (1981).

Owing to the exceptional nature of the preservation of the Uppsala specimen, the morphology of *A. brevipes* can be clarified and its relationships with contemporary gekkotans considered in more detail. These lizards are of some importance since they represent amongst the earliest 'modern' lizards with a fully developed kinetic skull.

The following acronyms are used: BMNH, British Museum (Natural History); CM, Carnegie Museum, Pittsburgh; PMU, Paleontological Museum, Uppsala.

SYSTEMATIC DESCRIPTION

Infra-order GEKKOTA Cuvier, 1817
Superfamily GEKKONOIDEA Underwood, 1954
Family ARDEOSAURIDAE Camp, 1923
Genus ARDEOSAURUS Meyer, 1860
Ardeosaurus brevipes Meyer, 1860

Plate 48

1855 *Homeosaurus brevipes* Meyer, p. 335.
1860 *Ardeosaurus brevipes* Meyer, p. 106, pl. 7.
1908 *Ardeosaurus brevipes* Nopcsa, p. 37.
1923 *Ardeosaurus brevipes* Camp, p. 306, fig. *c*.
1925 '*Homeosaurus* (*Ardeosaurus*) *brevipes* Meyer' Broili, p. 108.
1938 ?*Ardeosaurus brevipes* Broili, p. 105.
1953 *Ardeosaurus brevipes* Hoffstetter, p. 346, fig. 1*b*.

[Palaeontology, Vol. 25, Part 3, pp. 461–469, pls. 48–49.]

1955 *Ardeosaurus brevipes* Hoffstetter, p. 612, fig. 3*b*.
1963 *Ardeosaurus brevipes* Cocude-Michel, p. 145.
1964 *Ardeosaurus brevipes* Cocude-Michel, p. 704.
1964 *Ardeosaurus brevipes* Hoffstetter, p. 282.
1966 *Ardeosaurus brevipes* Hoffstetter, p. 592, fig. 1.

Holotype. The original described by Meyer (1855) is apparently lost, but a cast remains of the near complete, but poorly preserved specimen, BMNH no. 38006.

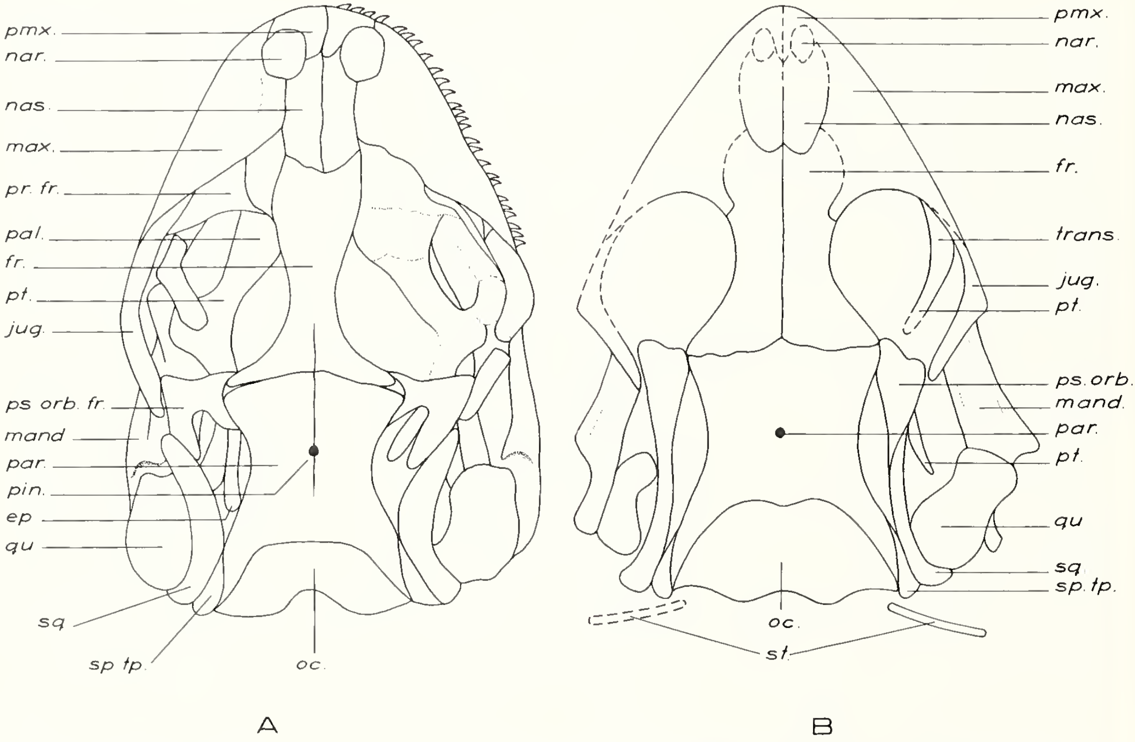
Horizon. Upper Kimmeridgian (Solnhofen Plattenkalk), Upper Jurassic.

Locality. The holotype and the present specimen (PMU.R58) are from the Eichstätt quarries, Bavaria, Federal Republic of Germany.

DESCRIPTION

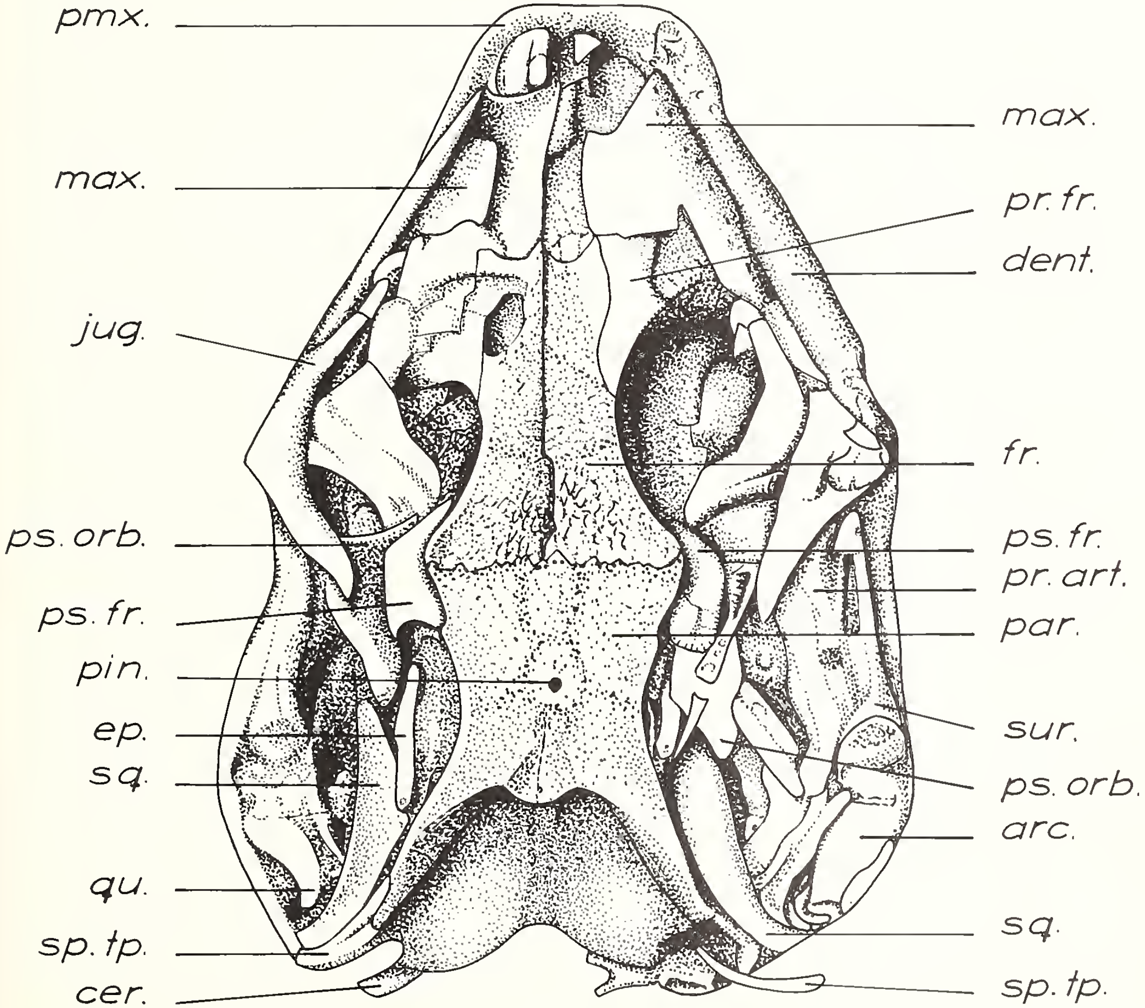
The new specimen is complete except for the distal part of the tail (Pl. 48). The preservation is mostly excellent, although it is dorso-ventrally compressed; relative to other specimens from the Upper Jurassic, it is exceptional. Since the other specimens are so poor and scarce, descriptions, photographs, and diagrams by Hoffstetter (1964, 1966) have been relied upon heavily in the comparisons made below.

Nearly all the bones from the dorsal surface of the skull are clearly defined (text-figs. 1*b*, 2; Pl. 49, figs. 1, 2, 3). The overall shape is triangular anterior to the parietals, but with a slightly squared margin. The narial



TEXT-FIG. 1. Comparative outlines of (*a*) *Eichstaettisaurus schroederi* (Munich 1937-I-1) × 2·5, (*b*) *Ardeosaurus brevipes* (BMNH. 38006) × 3·5. ep, epipterygoid; fr, frontal; jug, jugal; mand, mandibular; max, maxillae; nar, narial; nas, nasal; oc, occipital; pal, palatine; par, parietal; pin, pineal; pmx, premaxillae; pr.fr, prefrontal; ps.orb, postorbital; ps.orb.fr, postorbito-frontal; pt, pterygoid; qu, quadrate; sp.tp, supratemporal; sq, squamosal; st, stapes; trans, transpalatine.

openings are relatively large and oval, set almost parallel to the midline. The premaxillae are not clearly seen but appear, nevertheless, to be paired. The nasals are quite short and straight-sided; the outer border of these bones, however, are somewhat obscured by the dorsal processes of the maxillae concealing their true shape. The maxillae meet the jugals at a short concave suture. The prefrontals are large and extend anteriorly to halfway between the anterior border of the orbit and the premaxilla border. They comprise almost the entire anterior arc of the orbit. The anterior border of the prefrontals is not clearly seen along its full extent, but it would appear to be rather broad, extending antero-laterally further than in *Eichstaettisaurus*. The lachrymals are absent. The frontals are paired along their full length and are straight-sided after the initial constriction anterior to the parietal contact, which finishes at the mid-orbital level. The sinuous nature of the naso-frontal contact suggests that this was not a kinetic joint. The jugals are moderately robust and have a boomerang-shape. The posterior end of the jugal articulates with the postorbital tapering on the inner side. The components of the postorbito-frontal complex (Hoffstetter 1964) are here clearly separate entities, but nevertheless do complete the postorbital arc. Anteriorly, the postfrontal flutes narrowly into the orbital border of the frontal;



TEXT-FIG. 2. Skull of *Ardeosaurus brevipes* (Meyer) (PMU.R58). ×6·4. arc, articular; cer, ceratohyal; dent, dentary; pr.art, prearticular; ps.fr, postfrontal; sur, surangular (other abbreviations, see text-fig. 1).

it expands posteriorly to form the anterior margin of the supratemporal foramen. It is triangular and connects the jugal and postfrontal to the squamosal. The postorbital of the type of *A. brevipes* is poorly known, but a clear similarity is apparent with the Uppsala specimen; the postorbital and postfrontal in *Eichstaettisaurus* has a quite different form (text-fig. 1*a* is based upon a reconstruction by Hoffstetter (1967); Estes (1981) holds that the postorbital and postfrontal are separate bones, not fused as Hoffstetter showed). The supratemporal foramen is typically elongate, bordered by the constricted parietal on the inner side, and by the postorbitofrontal and squamosal on the outer side.

The squamosal is substantial and evenly curved resembling a 'hockey stick' (Robinson 1967), although this shape may vary with the preserved aspect. The nature of the contact to the quadrate is not clear, although the peg for insertion into the quadrate notch can be distinguished. This latter notch is not seen. The supratemporal separates the posterior part of the squamosal from the paroccipital.

The parietal is square with moderately robust paroccipitals; these latter have a very slight tendency to incline inwardly, otherwise being quite straight. The parietals are co-ossified and the pineal opening lies centrally and is quite small. The substantial suture between the parietal and the frontals is straight transversely and the marked fracture along this contact suggests a certain weakness, or previous mobility, indicating that mesokinesis (a hinging of the snout relative to the posterior part of the skull) was fully developed in *Ardeosaurus*. Thus, this specimen would appear to be a rather typical amphikinetic lizard. The left and right epipterygoids are preserved appearing through the supratemporal foramena; they are slim rod-like bones, showing a kink midway along the shaft.

The occipital region is not well preserved and the definition of the components is difficult. Notwithstanding, this is reconstructed (text-fig. 3). The paroccipitals extend around to articulate with the full length of the supratemporals and meet the quadrates which are obscured by the squamosals. What can be seen of the quadrates, shows that they are not broad and a longitudinal groove may indicate the presence of a notch on the dorsal surface. There is no quadratojugal connecting the jugal with the quadrate to form a lower temporal bar; this indicates a streptostylic condition. The left hyoid is preserved lying near the left paroccipital.

Osteoderms and epidermal scutes are present on the frontals and the anterior half of the parietal (Pl. 49, fig. 1). Four epidermal scutes are recognizable; most notable is the interparietal scute which is split into an anterior and posterior part, in contrast to the normal single interparietal. The anterior borders of the frontal epidermal scutes are not seen. The frontoparietal and parietal scutes are more apparent. The markings are not characteristic of the Gekkota and Iguania, rather they show similarity to those of the Scincomorpha (Estes 1981). Hoffstetter (1964) mentioned minor rugosities or granulations indicating the possibility of osteodermal sculpture in *A.* cf. *digitatellus*.

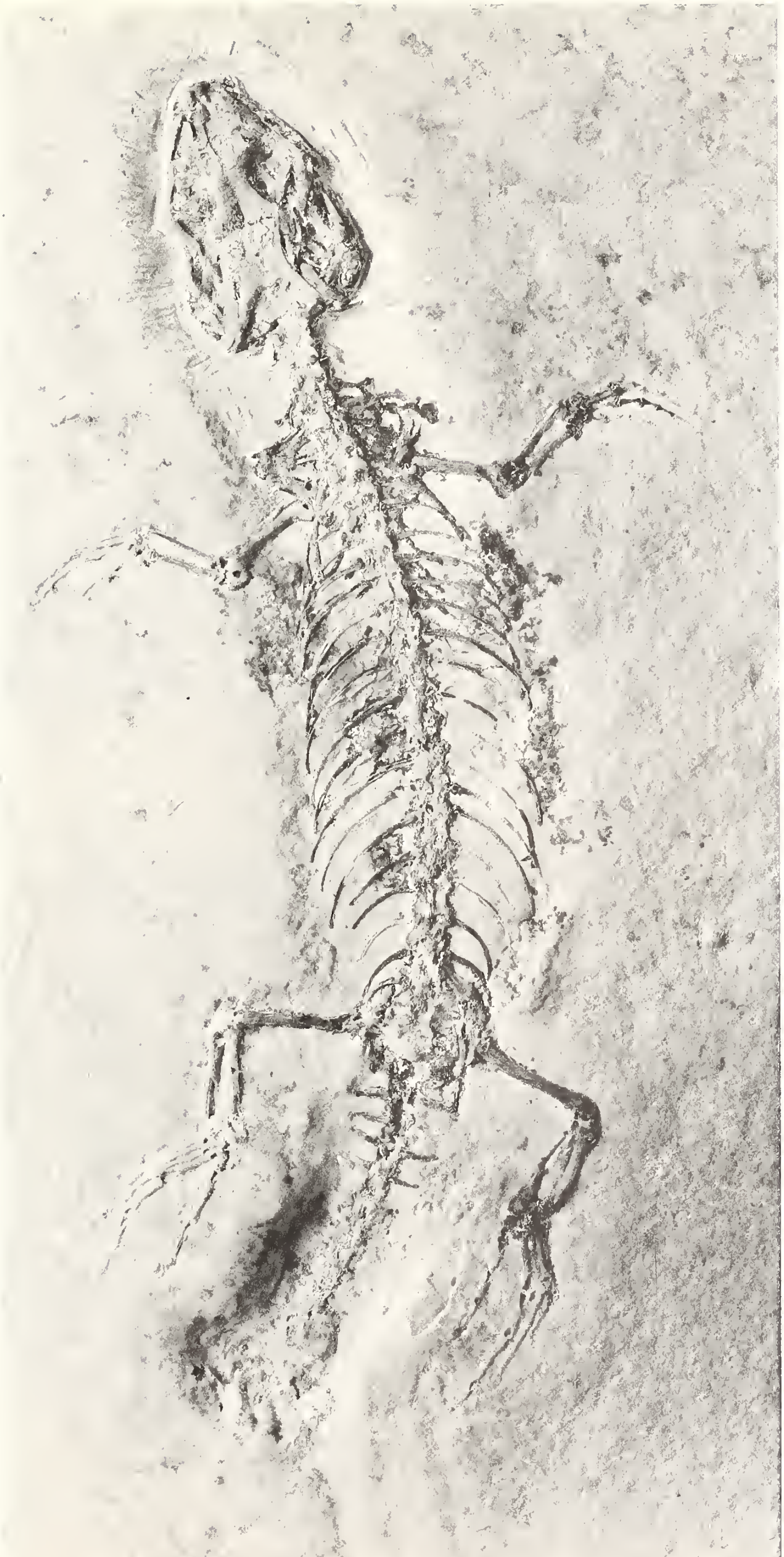
No teeth are sufficiently well preserved to state the type of dentition *Ardeosaurus* had. There are traces of teeth on the right dentary (not visible in Pl. 49, fig. 2) which would appear not to be acrodont; presumably, in common with most lizards, *Ardeosaurus* had a pleurodont dentition.

Twenty-three presacral vertebrae are present and only some ten poorly preserved caudals, excluding the two sacral vertebrae. The dorsal series do not vary much in size and their centra are procoelous and rather broad. Twenty-two pairs of ribs are seen. The pectoral is badly dislocated (Pl. 49, fig. 4). Owing to poor preservation and a lack of comparative material, the structure of the girdle is not clear. The coracoid, lying posteriorly, is relatively slim compared with recent forms (Hoffstetter 1964, fig. 4). A coracoid window is present, although the exact form is not certain. The scapula appears only a little thinner than the postero-palinal process, and has become detached from the anterior part of the coracoid during preservation. The glenoid cavity has been extensively re-mineralized. Although the pelvic girdle is poorly preserved, it appears to be very similar to that figured by Cocude-Michel (1963, fig. 39*a*) for *A. digitatellus*.

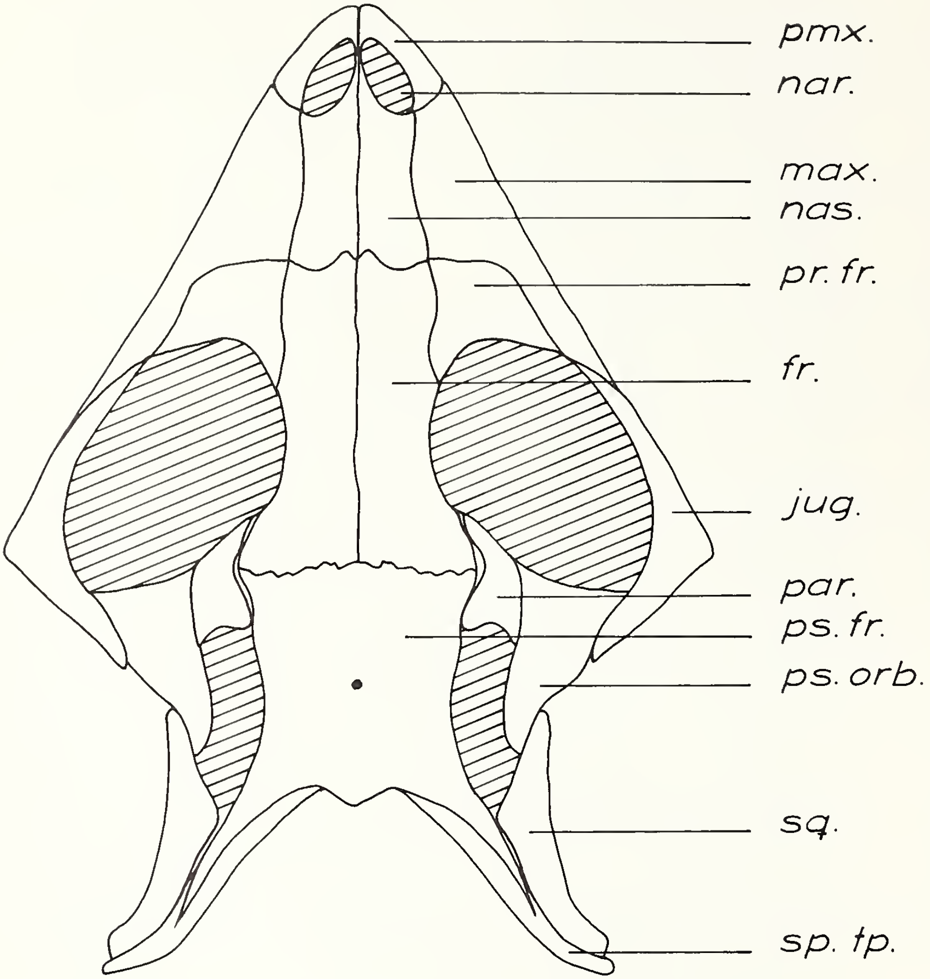
All four limbs are largely complete, though the tarsi and carpi have been extensively re-mineralized. The astragulus and calcaneium have not co-ossified and this indicates a juvenile condition. The phalangeal formula is 2-3-4-5-3/2-3-4-5-3; the first digit is slightly obscured by the overlying second digit, but there appear to be two phalanges.

EXPLANATION OF PLATE 48

Dorsal view of *Ardeosaurus brevipes* (Meyer) (PMU.R58) from the Upper Jurassic of southern Germany. × 1·4.



MATEER, Jurassic lizard



TEXT-FIG. 3. A cranial reconstruction of *Ardeosaurus brevipes* dorsal view, based on *A. brevipes* (Meyer) (PMU.R58) in Uppsala. See text-fig. 1 for explanation of abbreviations. ×6·4.

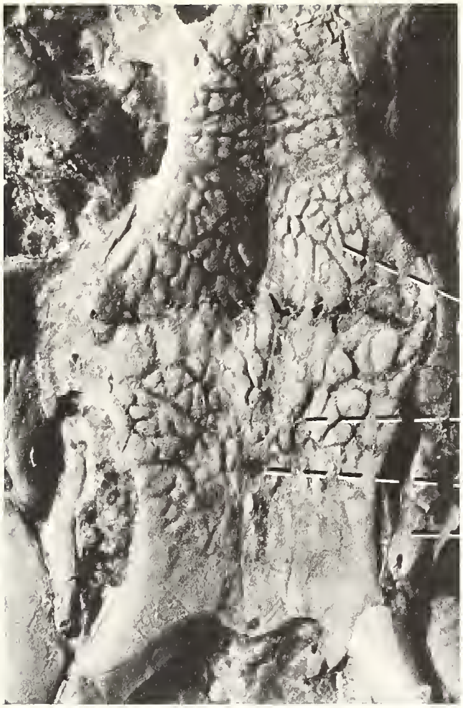
EXPLANATION OF PLATE 49

Fig. 1. Dorsal view of the parietal and posterior frontals of *Ardeosaurus brevipes* (Meyer) (PMU.R58) showing the position of the pineal opening and the nature of the osteoderms. See text-fig. 1 for explanation of abbreviations. ×6·70.

Fig. 2. A detailed dorsal view of *Ardeosaurus brevipes* (Meyer) (PMU.R58). See text-fig. 1 for explanation of abbreviations. ×3·25.

Fig. 3. A detailed view of the left quadrate suspensorium of *Ardeosaurus brevipes* (Meyer) (PMU.R58). See text-fig. 1 for an explanation of abbreviations. ×6·70.

Fig. 4. A dorsal view of the left pectoral girdle of *Ardeosaurus brevipes* (Meyer) (PMU.R58). cor, coracoid; hum, humerus; sca, scapula. ×6·70.



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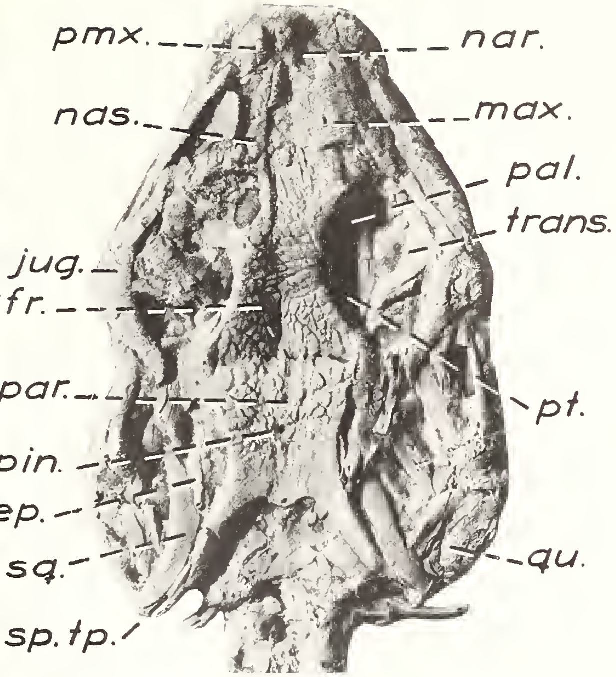

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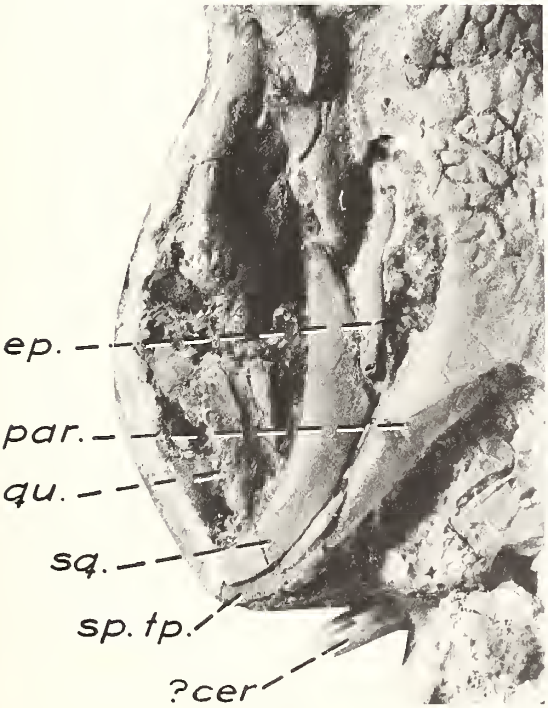

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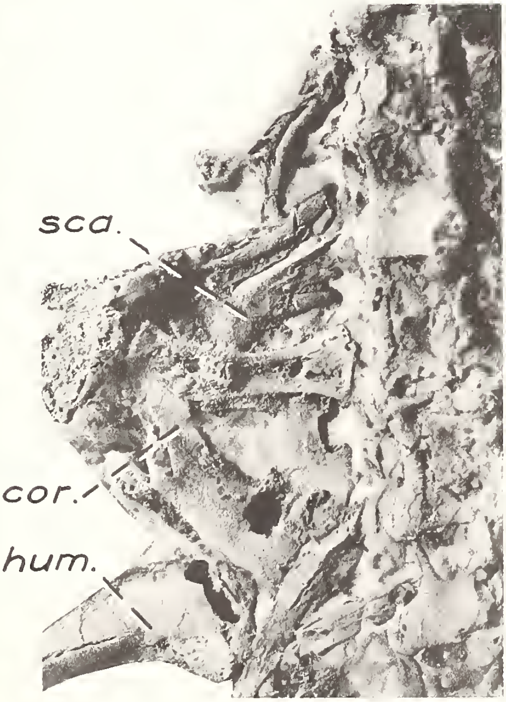

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MATEER, Jurassic lizard

DISCUSSION

Characters that have not previously been seen, or clearly seen, in this species and genus that are revealed in this specimen include: osteoderms on the frontals and parietal; separated postfrontal and postorbital; a complete postorbital arc; epipterygoids; paired nasals and the nasal-premaxilla contact; the narial openings; straight-sided frontals and large prefrontals.

The poor preservation of the two specimens of *A. digitalellus* makes an accurate comparison with *A. brevipes* difficult. Nevertheless, the following minor differences are noted with respect to *A. brevipes*: a less pointed snout; the width to length ratio of the parietal is somewhat higher, giving a more squared shape; the jugals are less robust but more curved; the ratios humerus plus ulna to manus/femur plus tibia, to pes, differ: 1·0/1·4 in *A. digitalellus*, and 1·3/1·2 in *A. brevipes*. These differences are minor and would appear not to carry much taxonomic weight, thus the retention of these two species of *Ardeosaurus* is seriously questioned. Hoffstetter (1964) suggested that *A.* cf. *digitalellus* may be an adult form of *A. brevipes*, but this is difficult to justify.

Three further genera of lizard are also known from the Upper Jurassic of Germany: *Eichstaettisaurus*, *Bavarisaurus*, and *Palaeolacerta*, of which only *Eichstaettisaurus* is known from a good specimen. These various specimens are reviewed in detail by Hoffstetter (1964) and Estes (1981). The differences between *Ardeosaurus* and *Eichstaettisaurus* are clear despite some confusion in the previous literature. *Eichstaettisaurus* has a much larger and more rounded snout with a depressed anterior margin; the orbits are much larger and are placed more posteriorly than in *Ardeosaurus*; the frontals are fused and very narrow giving rise to a pronounced expansion toward the parietal border; *Ardeosaurus* has only twenty-three to twenty-five presacral vertebrae versus thirty in *Eichstaettisaurus*; a different shape to the supratemporal foramen is caused by the much shorter postorbital and postfrontal; longer nasals than in *Ardeosaurus*; and a partially sutured parietal (text-fig. 1*a*). This emphasizes Hoffstetter's defence of keeping *Ardeosaurus* and *Eichstaettisaurus* separate, *contra* Cocude-Michel's (1965) suggestion that they are synonomous. (See also Estes 1981.)

The genus *Yabeinosaurus* from the Upper Jurassic of Manchuria, China (Endo and Shikama 1942; Young 1958; Hoffstetter 1964), shows a very close association with *Ardeosaurus* and *Eichstaettisaurus*. The differences are primarily proportional, except for the following: a very large orbit in which the jugals do not meet the postorbital to complete the postorbital arc; a very small pineal opening; a very short and broad postorbito-frontal, not unlike that of *Eichstaettisaurus*, giving a broad supratemporal foramen; a smaller and more posteriorly placed parietal; twenty-eight presacral vertebrae, and relatively short limbs.

Bavarisaurus and *Palaeolacerta*, though in general similar, are distinguishable from the above genera. *Palaeolacerta* has a more elongate skull, larger and less anteriorly placed orbits, and amphicoelous vertebrae. The supposed large pineal opening near the fronto-parietal border is thought to be an artifact (Estes 1981). *Bavarisaurus* also has amphicoelous vertebrae, a greatly enlarged supratemporal foramen, an apparent absence of a pineal opening, and remarkably long limbs. The type, and only specimen, is not well preserved, thus the absence of a pineal (which lies in an area of breakage) should be treated tentatively; the amphicoelous vertebrae, however, are significant.

The relationships of the Ardeosauridae and Bavarisauridae to the early history of the gekkotans are not clear. Estes (1981) discusses characters that these families share in common with both the Gekkota (generally recognized as one of the most primitive of lizards) and the Scincomorpha. The epidermal scutes seen in the Uppsala specimen of *Ardeosaurus* suggest that the Ardeosauridae, comprising *Ardeosaurus*, *Eichstaettisaurus*, and *Yabeinosaurus*, should be assigned to the Scincomorpha (see Robinson 1967) thus indicating possible relationships between the Gekkota and Scincomorpha (Estes 1981). In the absence of sufficiently well-preserved early specimens, a conservative course is taken here, placing these families within the Gekkota.

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FOSSIL BONE RECOVERY FROM SEDIMENT RESIDUES BY THE 'INTERFACIAL METHOD'

by ERIC F. FREEMAN

ABSTRACT. New methods for the separation of microvertebrate fossils from particulate sediment residues are based on preferential wetting of the bone particles by water-immiscible solvents in aqueous media. Three embodiments of this basic idea are described, two of them involving adhesion of the bone particles to solid or gelatinous materials (polystyrene or high molecular weight hydrocarbons), whilst the third relies on simple two-phase liquid mixtures. The new methods give results which compare favourably with those from conventional techniques of bone-enrichment, and at minimal or negligible cost. In small-scale experiments, efficient separation of bone has been achieved from gangue minerals consisting largely of quartz, limonite, calcite, siltstone, and claystone, and of particle sizes ranging between 1·4 mm and 0·35 mm. Multi-stage separations are possible, allowing one to obtain high-purity concentrates virtually quantitatively from sediment residues of low initial bone content. One such exercise is demonstrated on the large-scale, using 1 kg of quartz-rich sediment residues.

The use of a new reagent, sodium hydrogenoxalate, for the digestion of limonitic gangues, is briefly described, as are improvements relating to conventional bromoform density separations.

IN recent years microvertebrate fossils have attracted increased attention from palaeontologists, due in large part to a growing interest in the origins of the major vertebrate groups, the early representatives of which tended to be small animals. Also, as small vertebrates are often important ecologically, and as they frequently consist of the young of larger animals, their fossil remains would be expected to yield data important in the reconstruction of ancient environments and animal communities. Also, microvertebrates can be useful in stratigraphy.

The recovery of microvertebrate fossils from a sediment typically involves a three-stage process, requiring the palaeontologist (1) to disaggregate the sediment to give a particulate residue of the relevant size-range, from which (2) unwanted gangue minerals are removed by a variety of processes to give a bone-enriched concentrate, which (3) is hand-picked for specimens of interest. Unfortunately, the bone-enrichment processes hitherto available for stage 2 are usually not very cost-effective, and the yield of microvertebrates from a sediment is often limited by the then inevitably tedious nature of stage 3.

Bone-enrichment processes fall roughly into two categories, depending on whether the gangue minerals are removed chemically or physically. Chemical methods include the dissolution of calcareous gangues with acetic or formic acid solutions (see Rixon 1976) and of limonitic gangues using thioglycollic acid (Freeman 1979, following Howie 1974). Physical methods include 'jigging' on a sieve in water (for lignite—Kühne 1968), flotation in either chlorinated hydrocarbons (for lignite—Freeman 1975) or brominated hydrocarbons (usually for quartz—see, for example, Griffith 1954), and use of a photoelectric scanner to separate bone and gangue particles by means of their colour differences (Kühne 1970). All these techniques have one or more drawbacks, usually limited applicability, low efficiency, high cost, and reagent hazard.

Whilst engaged in a search for mammal teeth in a Lower Cretaceous bone bed, I have developed a suite of remarkable new procedures which allow bone-bearing sediment residues to be enriched with higher efficiency and/or much lower cost than any other method previously described. As these procedures exploit phenomena at the interfaces of mutually immiscible liquids, I have named them collectively the 'Interfacial Method'.

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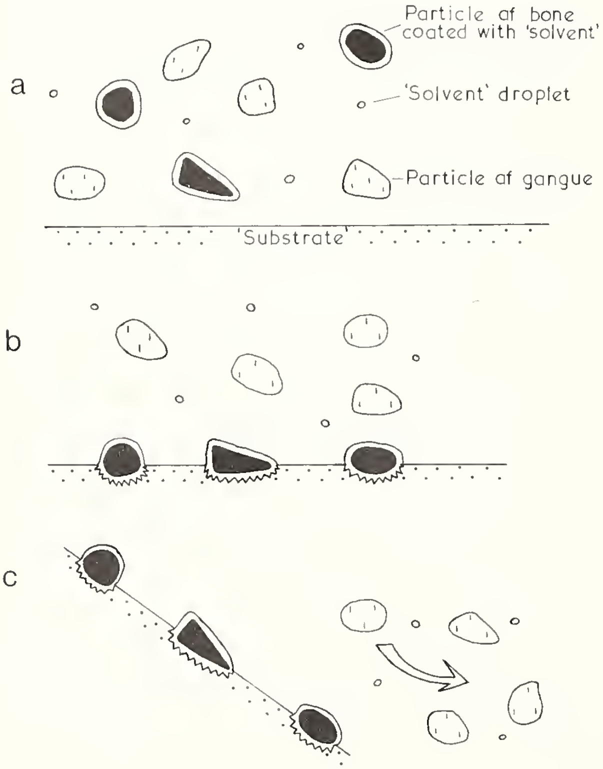
THE INTERFACIAL METHOD—GENERAL DESCRIPTION

The new procedures are all based on a seemingly unknown property of fossil bone, namely that when contacted with a two-phase mixture of water and a water-insoluble organic liquid, it is wetted by the organic liquid more readily than are the gangue minerals. Three general procedures, differing only in the way that this phenomenon is exploited, have been investigated experimentally, and are described herein.

In two of these, called Procedures A and B, the particulate bone-bearing residue is gently agitated with a suspension of the water-insoluble organic liquid (hereafter for brevity called the 'solvent') in a dilute aqueous detergent solution, whereupon the particles of bone become preferentially coated with the 'solvent'. The mixture is then briefly brought into contact with a 'substrate', a solid or gelatinous material whose composition is such that it softens in contact with the 'solvent' (see text-fig. 1*a*). When the bone particles make contact with such a 'substrate', they become attached to it by means of their 'solvent' coatings (see text-fig. 1*b*). Subsequent removal of the unattached material leaves a concentrate enriched in bone particles adhering to the surface of the 'substrate' (see text-fig. 1*c*).

In more detail, the 'substrate' of Procedure A consists of polystyrene, a low-cost polymer widely used in food-packagings; the 'solvent' can be one of a number of suitable aromatic or chlorocarbon solvents, but is preferably tetrachloroethylene, a relatively inexpensive dry-cleaning agent. The concentrate adhering to the polystyrene is removed either by gentle brushing (after rinsing with light petroleum spirit and air-drying), or if it is too firmly attached, by dissolving the polymer in a suitable solvent. Alternatively, the concentrate may be searched *in situ* for specimens of interest.

In Procedure B, the solvent is even cheaper, being domestic paraffin (kerosene), while the 'substrate' is a high molecular weight solid or gelatinous hydrocarbon such as either petroleum



TEXT-FIG. 1. The mechanism of the Interfacial Method, Procedures A and B. In aqueous suspension, particles of fossil bone are selectively coated with water-insoluble organic solvent (*a*), which allows them to adhere to a suitable 'substrate' (*b*). Removal of the unattached gangue minerals (*c*) leaves a concentrate of bone particles on the surface of the 'substrate'.

jelly (which is coated on to a suitable, inert support) or paraffin wax. The concentrates from Procedure B are recovered by melting the 'substrate' materials in hot water containing a little detergent. This also allows the 'substrate' materials to be recovered for reuse, at a considerable saving in cost.

In the third procedure described in this paper, called Procedure C, the sediment residue is briefly agitated with a simple mixture of tap water (*not* containing detergent) and an immiscible organic liquid (in practice, domestic paraffin), which is then allowed to settle momentarily. The interface between the two liquids holds in suspension a small quantity of material enriched in bone, which is recovered merely by decanting the liquids through a fine wire mesh.

As to their effectiveness, Procedures A and B have given concentrates which may be hand-picked without the need of further enrichment. This is not true for Procedure C, where the degree of enrichment achieved so far, although potentially useful, has not been spectacularly high. However, its fundamental simplicity and the low cost of its materials make Procedure C an attractive prospect for large-scale mechanized sediment processing.

Procedures A, B, and C are described in more detail in the 'Experimental' section (following).

EXPERIMENTAL

The following account describes firstly a limited investigation on the small-scale of some of the more obvious variables relating to the new procedures, the information from which is then used in larger-scale experiments more appropriate to the practical needs of the palaeontologist.

The overall performance of an experiment was measured by three parameters, the relative percentages of bone in the starting material and in the resulting concentrate, and the percentage of the bone originally present in the test sample that was recovered in the concentrate (called hereafter the 'recovery of bone'). The percentage compositions of the starting materials and the products were estimated by hand-sorting representative samples, usually under natural daylight and using low-power magnification. Under such conditions, identification of the bone particles did not present much of a problem, except when the gangue was lignite (Experiment 8). Unless indicated to the contrary, for the small-scale experiments the percentage compositions and bone-recoveries are based on the numbers of particles (rather than on their weights); the exceptions are where the gangue particles were fragile and liable to disintegration during the experiment.

In the tables, to facilitate comparison the starting material weights have been standardized to 5·00 g or 25·00 g; similarly the term 'concentrate' covers *all* residues which either adhere to a 'substrate' (for Procedure A) or are carried over by decantation (for Procedure C), irrespective of whether any enrichment of bone has in fact occurred (see, for example, Experiment 33).

Finally, for simplicity the term 'bone' is used in a loose sense to cover all phosphatic fossils, including teeth and coprolites.

THE ORIGIN OF THE EXPERIMENTAL MATERIALS

To make the experiments as realistic as possible, actual residues obtained from sediment processing were used in preference to 'tailor-made' mineral mixtures, which in some ways would have made for more 'elegant' experiments. Emphasis was placed on quartz-rich residues of 0·5–1·0 mm particle size, largely because such materials are especially laborious to search manually and yet often contain specimens of interest.

Details of the procedures used to break down the sediments are given, as these, by affecting the surface properties of the resulting particulate residues, might have had an influence on the experimental results.

?Telham Bone Bed. This sediment is a thin pebbly ferruginous sandstone, found attached to the upper surfaces of massive blocks of fine-grained sandstone fallen from East Cliff, Hastings (map reference TQ 832096). It is suspected to be the Telham Bone Bed from the descriptions given in Allen 1949, pp. 279–282 and Allen 1962, pp. 224–225. If so, it is part of the Wadhurst Clay Formation, and probably is of Valanginian age (Lower Cretaceous) (see Clemens and Lees 1971, pp. 120–121). So far, 12·5 kg of the sediment has yielded at least four mammal teeth, as yet undescribed, as well as remains of fish (*Lepidotes*, *Hybodus*, *Lonchidion*, and *Hylaeobatis*), turtles, crocodiles (goniopholids and *Bernissartia*), and dinosaurs (*Iguanodon* and *Megalosaurus*).

After digestion with dilute acetic and formic acid solutions, the particles in the resulting residues were still heavily coated and partially aggregated by a tenacious limonitic cement. As the Interfacial Method exploits the surface properties of the fossil bone particles, obviously they must not be attached to, or coated with, substantial amounts of such gangue minerals. The limonitic cement was removed from the 0·5–1·0 mm fraction by digestion in 10·0 g batches with 150 ml portions of concentrated sodium hydrogenoxalate solution at *c.* 100 °C for an hour. The oxalate solution was prepared by the partial neutralization of oxalic acid (10·0 g of the anhydrous acid) with sodium bicarbonate (9·3 g) in 150 ml of calcium-free water. Its reactivity towards limonite represents the satisfactory compromise between oxalic acid solution, which dissolves limonite but also attacks fossil bone, and sodium oxalate solution, which is inert. As a reagent for limonite, sodium hydrogenoxalate offers considerable advantages of cost and general convenience over thioglycollic acid (see Howie 1974 and Freeman 1979).

After the oxalate digestion, the 0·5–1·0 mm material consisted of a mixture of clean and separate quartz, limonite, and bone particles. It was used in most of the small-scale experiments (nos. 1, 2, 9–33), either as such, or after further separation by conventional bromoform flotation and/or the Interfacial Method.

Cliff End Bone Bed. This material, of similar age to the Telham Bone Bed, occurs as loose blocks of coarse ripple-marked sandstone at Cliff End, Kent. It too contains mammal teeth, which in recent years have been collected by systematic processing involving acid-digestion and heavy-liquid density separation (see Clemens 1963, Kermack, Lees and Mussett 1965, and Clemens and Lees, 1971). Kermack *et al.* mentioned the recovery of nine mammal teeth from 5 cwt. (254 kg) of matrix using such methods.

The material used for the scaled-up Interfacial Method separations (Experiments 34–9) was part of that yielded by digestion of 58 kg of the Cliff End Bone Bed with dilute formic and acetic acid solutions. It consisted largely of separate, clean particles of quartz and fossil bone, and thus did not require any after-treatment, except for thorough washing with water and detergent to remove fine dust.

Kirtlington Mammal Bed. This is a thin bed of mammaliferous marl within the Forest Marble (Middle Jurassic) of the Old Cement Works Quarry, Kirtlington, Oxfordshire (see Freeman 1979, and Ware and Whatley 1980).

The material used for Experiment 4 was produced by wet-sieving of the sediment, and consisted largely of a mixture of comminuted shell fragments and ooliths. Experiment 3 used the insoluble limonitic residue from acetic acid digestion of such a washing residue.

'*Cowleaze Chine Pellet Bed*'. This is an undescribed channel deposit at the base of the Wealden Shales (Lower Cretaceous), near the mouth of Cowleaze Chine, Isle of Wight (map reference SZ 443801). It consists of a small lenticular mass of clay pellets in a calcareous siltstone matrix, and was disaggregated using dilute acetic acid solution to give the material used for Experiment 5. The vertebrate fauna consists principally of elasmobranchs, and was itemized in Freeman 1975 (Table 1, under 'Undescribed channel deposit').

Perna Bed. This is a glauconitic sandstone, rich in marine molluscs and corals, and locally, in fish bones and teeth, at the base of the Lower Greensand (Aptian, Lower Cretaceous) in the Isle of Wight. The particular sample used in Experiment 6 came from Atherfield Point—see Osborne White 1921, p. 24, and was disaggregated using dilute acetic acid solution.

Cyrena Limestone. This is a thin-bedded silty limestone crowded with freshwater lamellibranchs, occurring repeatedly within the Wealden Shales (Lower Cretaceous) of the Isle of Wight (see Osborne White 1921, p. 15). The particular sample used for Experiment 7 was found loose on the beach south-east of Shepherd's Chine (map reference SZ 448796), and was broken down with dilute acetic acid solution.

'*Headon Hill Lignite Bed*'. This is an irregular seam of friable, mammaliferous lignite in the Upper Headon Beds (Upper Eocene) of Headon Hill, in the Isle of Wight (see Cray 1973, pp. 24–27). The material used for Experiment 8 was obtained by wet-sieving the sediment.

PROCEDURE A

A typical small-scale experiment (*Experiment 1*)

A 5·00 g sample of 0·5–1·0 mm residue from the ?Telham Bone Bed, containing 13% bone, was saturated with tetrachloroethylene (2·6 g, 1·6 ml), and agitated briefly in a 250 ml 'Pyrex' beaker with 50 ml of a 1% solution of a proprietary 'washing-up liquid' ('Fairy Liquid', ex Procter and Gamble Ltd.) in cold tap-water. The mixture was then poured rapidly from the beaker into a

160 ml container made of unfoamed polystyrene (an empty yogurt carton), where it was kept for *c.* 15 seconds, before being transferred as completely as possible to another such container. The surfaces of the polystyrene that had come into contact with the mixture had been somewhat corroded and softened by the tetrachloroethylene, and to them adhered a concentrate consisting predominantly of fossil bone particles. The process was repeated another five times, the yield and purity of the concentrates attached to the polystyrene decreasing steadily in amount and purity from the first container to the sixth. In total, the concentrates weighed 0·43 g, contained 78% of bone and constituted a bone recovery of 85%. The material that did not become attached to the polystyrene (the tailings) weighed 4·57 g, and contained 2·1% of bone.

The nature of the sediment residue and 'solvent' type in Procedure A separations (*Experiments 1–21*)

Using the above method, various aspects of Procedure A have been investigated experimentally. Enrichment in bone has been achieved for sediment residues consisting largely of quartz, limonite, calcite (ooliths and shell fragments), claystone, and siltstone (see Table 1, Experiments 1–6), of particle sizes ranging between at least 0·35 mm and 1·4 mm (Experiments 9 and 10), and containing as much as 61% of bone (Experiment 11) and as little as 0·8% (Experiment 12). Only the separation

TABLE 1. The scope of the Interfacial Method, Procedure A. Abbreviations: ?TBB = ?Telham Bone Bed; KMB = Kirtlington Mammal Bed; CCPB = 'Cowleaze Chine Pellet Bed'; PB = Perna Bed; CL = Cyrena Limestone; HHLB = 'Headon Hill Lignite Bed'; C_2Cl_4 = tetrachloroethylene. All the percentages quoted for Experiments 3, 7, and 9 are based on the weights of the particles, and not on their numbers. The experimental procedures were as described for Experiment 1.

STARTING MATERIAL (5·00g)					SOLVENT	TAILINGS		CONCENTRATE		
Expt. no.	Source	Chief gangue mineral(s)	Particle size	% bone	Volume of C_2Cl_4	Wt.	% bone	Wt.	% bone	Recovery of bone
1	?TBB	99% quartz	0·5–1·0 mm	13%	1·6 ml	4·57g	2·1%	0·43g	78%	85%
2	?TBB	95% limonite	0·5–1·0 mm	9·1%	1·6 ml	4·69g	3·5%	0·31g	91%	41%
3	KMB	97% limonite	0·5–1·0 mm	31%	4·0 ml	3·86g	23%	1·14g	52%	39%
4	KMB	88% calcite	0·5–1·0 mm	1·0%	1·5 ml	4·89g	0·8%	0·11g	6·2%	18%
5	CCPB	89% claystone	0·5–1·0 mm	1·3%	1·6 ml	3·87g		1·13g	6·2%	42%
6	PB	37% siltstone, 62% quartz	0·5–1·0 mm	4·3%	1·5 ml	4·72g	2·8%	0·28g	21%	33%
7	CL	c.100% pyrites	0·5–1·0 mm	19%	1·2 ml	4·38g	16%	0·62g	31%	20%
8	HHLB	94% lignite	0·5–1·0 mm	2·8%	0·8 ml	4·21g		0·79g	3·8%	28%
9	?TBB	limonite>quartz	1·0–1·4 mm	7·3%	3·1 ml	3·78g	1·7%	1·22g	25%	83%
10	?TBB	51% quartz, 49% limonite	0·35–0·5 mm	12%	1·6 ml	4·83g	8·9%	0·17g	83%	43%
11	?TBB	limonite	0·5–1·0 mm	61%	1·6 ml	1·12g	9·6%	3·88g	83%	97%
12	?TBB	quartz	0·5–1·0 mm	0·8%	1·8 ml	4·72g	0·5%	0·28g	5·5%	57%

TABLE 2. The results of two three-stage Procedure A separations. The experiments are continuations of Experiment 1 (*top*) and Experiment 2 (*bottom*), the starting materials for stages 2 and 3 being the tailings from stages 1 and 2 respectively.

STARTING MATERIAL			STAGE 1	STAGE 2	STAGE 3	RECOVERY OF BONE
?Telham Bone Bed, 0·5–1·0 mm., 13% bone, 86% quartz.	% bone in	concentrate	78	52	5·5	85+8+4 = 97%
		tailings	2·1	0·8	0·5	
?Telham Bone Bed, 0·5–1·0 mm., 9·1% bone, 86·0% limonite, 4·9% quartz.	% bone in	concentrate	91	23	1·5	41+49+8 = 98%
		tailings	3·5	0·9	0·5	

of bone from pyrites and lignite (Experiments 7 and 8) has proved difficult, apparently because these gangue minerals are nearly as readily wetted by the tetrachloroethylene 'solvent' as is the bone.

Multiple-stage extractions are possible (see Table 2), permitting the exhaustive extraction of a sediment for its microvertebrate content. As would be expected, the efficiency of a particular extraction is dependent upon the concentration of bone in the material being processed, and so a progressive decline occurs in the purity of the concentrates from stages 1 to 3.

A variety of chlorocarbon and aromatic 'solvents' have been used in Procedure A (see Table 3), of which the most successful was tetrachloroethylene. *Under the particular conditions prevailing*

TABLE 3. The variation of the nature of the 'solvent' in Procedure A separations. The experimental procedures were as described for Experiment 1.

STARTING MATERIAL;- 5·00g of ?Telham Bone Bed, 0·5–1·0mm fraction containing 13% bone and 86% quartz

Expt. no.	SOLVENT	TAILINGS		CONCENTRATE		
		Wt.	% bone	Wt.	% bone	Recovery of bone
1	1·6ml tetrachloroethylene	4·57g	2·1%	0·43g	78%	85%
13	1·8ml carbon tetrachloride	4·37g	3·1%	0·63g	40%	65%
14	1·1ml dichloromethane	4·74g	6·0%	0·26g	58%	44%
15	1·4ml chloroform	4·83g	7·7%	0·17g	70%	38%
16	1·4ml 1,2-dichloroethane	4·79g	8·9%	0·21g	83%	39%
17	1·7ml bromoform	3·05g	1·1%	1·95g	16%	92%
18	1·3ml xylene	4·44g	4·9%	0·56g	59%	80%
19	1·6ml toluene	4·72g	6·3%	0·28g	92%	58%
20	1·4ml benzene	4·96g	12%	0·04g	55%	6%
21	1·5ml paraffin	5·00g	13%	0·00g		0%

during an experiment the 'solvent' must have a positive, but only moderate, ability to attack the polystyrene 'substrate'. Consequently, Experiment 21, using paraffin, a non-solvent for polystyrene, failed because no material became attached to the 'substrate', while at the other extreme, when bromoform, an excellent solvent for polystyrene, was used, the polystyrene became coated with too much material, most of it gangue, and containing only slightly more bone than the starting material (Experiment 17). Presumably, a 'solvent' with optimum properties could be prepared by the judicious blending of two or more different solvents.

The quantity of the 'solvent'

All other factors being kept the same, one would expect the performance of a Procedure A separation to depend, not merely on the nature of the 'solvent' used, but also upon its quantity.

In the only case where this has been systematically studied (using the same, quartz-rich, experimental material as Experiment 23 (q.v.) and the method of Experiment 1), as the tetrachloroethylene was increased in amount from 1·5 ml to 2·0 ml, an increase in percentage recovery (from 28 to 42%) and a decrease in concentrate purity (from 85 to 69%) occurred. Curiously, these trends were not continued when the 'solvent' volume was further increased, eventually by sevenfold to 14 ml, the percentage recovery and concentrate purity remaining essentially static at 42 and 73% respectively.

In contrast, a few, limited experiments suggest that when the gangue mineral is limonite, pyrites, or lignite, increasing the quantity of 'solvent' produces dramatic increases in percentage recovery but with corresponding decreases in concentrate purity.

The necessity of a detergent in Procedure A (Experiment 22)

When detergent was omitted from a repeat of Experiment 1, the tetrachloroethylene remained as a discrete layer and did not disperse into fine droplets as before. Only a single polystyrene container was used, and to this became attached 0·99 g of material containing 33% of bone (cf. 78% in Experiment 1 and 13% in the starting material). So while a detergent greatly increases the efficiency of Procedure A, it seems not to be essential to it. The reverse is expected to be true for Procedure C.

Is there a 'palaeontological bias' in the Interfacial Method?

The Interfacial Method exploits subtle differences between the surface properties of the bone and gangue particles. It is even possible that differences in shape and texture between the bone particles themselves could be of significance. One would expect those bone particles having a relatively high surface area, such as flat fish scales and splinters of cancellous bone, to be the ones most readily wetted by the 'solvent', and therefore to be slightly more frequently recovered than would the relatively compact teeth of fish and reptiles. If so, in a multiple stage extraction, the proportion of the latter should progressively increase with each stage of the extraction. Interestingly, such an increase *has* been seen in one of the three-stage extractions reported earlier (see Table 4), and so this kind of 'palaeontological bias' should be borne in mind when using the Interfacial Method, although it is unlikely to be of major practical importance.

TABLE 4. 'Palaeontological bias' in a three-stage Procedure A separation. Note the progressive increase in the percentage of teeth (of *Lepidotes*, *Caturus*, *Lonchidion*, *Hybodus*, and crocodiles) in the concentrates from the three stages. The experiment is the continuation of Experiment 2 reported in Table 2, *bottom*.

STARTING MATERIAL:- ?Telham Bone Bed, 0·5–1·0mm fraction,
containing 9·1% bone, 86·0% limonite and 4·9% quartz

	STAGE 1	STAGE 2	STAGE 3	TAILINGS
Number of teeth	19	87	25	6
Total no. of bone particles	721	860	132	34
∴ Percentage of teeth	2·6%	10·1%	18·9%	17·6%

PROCEDURE B

A typical small-scale experiment (Experiment 23)

A 25·00 g sample of 0·5–1·0 mm residue from the ?Telham Bone Bed, containing 14% bone, 67% quartz, 16% limonite, and 3% lignite, was saturated with domestic paraffin (7·1 g, 9·2 ml) and washed into a 900 ml screw-cap bottle with 250 ml of a 1% solution of a proprietary washing-up liquid ('Fairy Liquid') in cold tap-water. A plastic cup, whose dimensions were such that it could be fitted snugly into the neck of the screw-cap bottle, had its base removed with a hot knife; it was then smeared heavily inside and out with petroleum jelly and inserted in the neck of the bottle. The bottle was then sealed, held horizontally, and agitated for 1 minute so that its contents played over the surface of the plastic cup. A small amount of a bone-rich concentrate remained stuck to the petroleum jelly on the cup, which was then rinsed in cold water to remove non-adherent material rich in gangue. This rinsing step is essential to maintain the richness of the concentrate—its omission in an otherwise identical experiment led to a reduction in the bone content of the concentrates (from the first ten extractions) from 56 to 27%.

In all, forty such extractions were performed, using a freshly prepared cup for each extraction. The plastic cups were then briefly immersed one by one in hot water containing a little detergent, whereupon the petroleum jelly melted and floated to the surface to form a curd, which was recovered for reuse. The bone-rich concentrates thus released accumulated in the bottom of the hot water bath.

Results. Concentrate from extractions 1–10: 3·45 g, 56% bone, recovery of bone = 76%.
Concentrate from extractions 11–40: 2·45 g, 14% bone, recovery of bone = 15%.
Tailings: 19·10 g, 1·2% bone.

Comparison of Procedure B with a density separation using bromoform

A fresh 25·00 g sample of the same material as that used for Experiment 23 was used in an essentially conventional heavy-liquid density separation (Experiment 24). Initially, this used neat bromoform (stabilized with ethanol, specific gravity 2·63–2·69), and gave a heavy fraction containing 20% of bone and weighing 4·13 g. A little ethanol was then added to lower the specific gravity to *c.* 2·57, and a second heavy fraction was obtained, this time containing 27% of bone and weighing 3·40 g. The procedure was, to some extent, optimized by being carried out in a 50 ml measuring cylinder, whose height : diameter ratio was more favourable to efficient use of the expensive flotation liquid and to clean separation of the heavy and light fractions than the beakers used by Kermack *et al.* (1965). In spite of this, separation of the bone was inefficient, as can be seen from Table 5, due to its wide density range, which overlapped those of the gangue minerals limonite and quartz.

Clemens and Lees (1971) describe some procedures for removing brominated hydrocarbons from flotation residues. These include washing in 70% alcohol in a fume cupboard, and drying in a vacuum oven evacuated through two vapour-traps cooled with liquid nitrogen. Whilst it is essential to remove all traces of brominated hydrocarbons from sediment residues prior to hand-picking because of their high toxicities (see, for example, bromoform in Sax 1975, p. 476), the use of a vacuum oven, etc., is unwieldy and expensive.

A much simpler procedure was developed to clean the residues from Experiment 24. Firstly, they were washed with methylated spirit and then water. They were then suspended in a fine wire mesh over a can of boiling water heated *out of doors*; this steaming procedure was continued until the steam issuing from the residues no longer smelt of bromoform. The procedure employs the technique of steam distillation (see Vogel 1956, p. 12) whereby water-insoluble organic compounds of high boiling-point can be vaporized at relatively low temperatures by admixture with steam. It was during one such bromoform-removal exercise in April 1979 that the Interfacial Method itself was discovered; ironically this will probably render the bromoform-density separation method largely obsolete, and with it the innovations reported in this section.

As a final precaution, the steamed residues were air-dried outdoors in strong sunlight, which should have served to oxidize photochemically any last traces of bromoform; alternatively, these could have been hydrolysed by treating the residues with a hot, dilute alkali solution.

The results of Experiment 24 are summarized in Table 5, and compared with those of the Procedure B separation described earlier. The overwhelming superiority of Procedure B is obvious from these results. Particular attention should be paid to the relative costs of the two methods and to the fact that Procedure B uses freely available materials which are virtually free of hazard. The only possible disadvantage of Procedure B compared to bromoform density separation is the relatively more energetic conditions it employs, which might increase the risk of damage to the fossils. In practice, I do not consider that this is a significant problem, as the particles of bone are initially cushioned against damage by the oily droplets enveloping them, and soon afterwards become embedded in the 'substrate'. Furthermore, the fossils isolated by Procedure B do not seem to be noticeably more fragmented than their counterparts isolated in other ways. In any event, the vastly increased quantity of sediment that can now be processed by Procedure B more than compensates for any specimens lost through breakage. This is true also for Procedures A and C, which employ less energetic conditions than Procedure B.

TABLE 5. A comparison of the performances of the Interfacial Method (Procedure B) and a conventional bromoform density separation. The costs are calculated from U.K. prices current at the time of the experiments (August 1979).

STARTING MATERIAL:- 25·00g of ?Telham Bone Bed, 0·5–1·0mm fraction, containing 14% bone, 67% quartz, 16% limonite and 3% lignite

	TAILINGS		CONCENTRATE			REAGENTS and COST
	Wt.	% bone	Wt.	% bone	Recovery of bone	
Interfacial Method, Procedure B, Expt. no. 23, extractions 1–10	21·55g	2·7%	3·45g	56%	76%	24g petroleum jelly £0·03 9·2ml paraffin £0·001
Conventional bromoform density separation (Expt. no. 24)	17·47g	7·0%	7·53g	23%	59%	18ml bromoform £1·18 0·8ml ethanol £0·0003

PROCEDURE C

A typical small-scale experiment (*Experiment 25*)

A 5·00 g sample of 0·5–1·0 mm residue from the ?Telham Bone Bed, containing 7·5% of bone and 91·5% of quartz, was placed in a 250 ml 'Pyrex' beaker, to which was added 25 ml of domestic paraffin and 25 ml of cold tap-water. Almost immediately thereafter, the water/paraffin mixture was decanted through a fine wire mesh (a tea-strainer), care being taken to ensure that the sediment residue at the bottom of the beaker did not slop over into the wire mesh. The interface between the two liquids held in suspension a small quantity of material enriched in bone, which was filtered off by the wire mesh. The water/paraffin mixture was returned to the beaker and the extraction repeated, in all for a total of 100 times over 15 minutes. In these extractions, vigorous agitation of the beaker and its contents tended to be counter-productive, adequate mixing being achieved simply by the return of the liquids to the beaker. A bone-enriched concentrate (0·77 g, 21% bone) accumulated in the wire mesh, leaving the tailings (4·23 g, 2·5% bone) in the beaker.

The effect of container geometry and solvent type upon Procedure C separations (Experiments 25–33)

Only two variables that might possibly have an effect upon Procedure C have so far been investigated, and both produced unexpected results. It was expected that the geometry of the container and of the liquids within it would be important factors in Procedure C separations. More specifically, the total area of the paraffin/water interface, and its vertical distance above the sediment residue should have a marked influence on the purity of the concentrate and on the percentage recovery of bone. However, contrary to such expectations, Experiments 26 and 27 both gave similar results to Experiment 25 (see Table 6), even though the interface areas and vertical distances ranged from 12 cm² and *c.* 22 mm for Experiment 26 to 87 cm² and *c.* 7 mm for Experiment 27.

TABLE 6. An investigation of container geometry and solvent type in Interfacial Method (Procedure C) separations. The experimental procedures were as described for Experiment 25 (except for the 'variable').

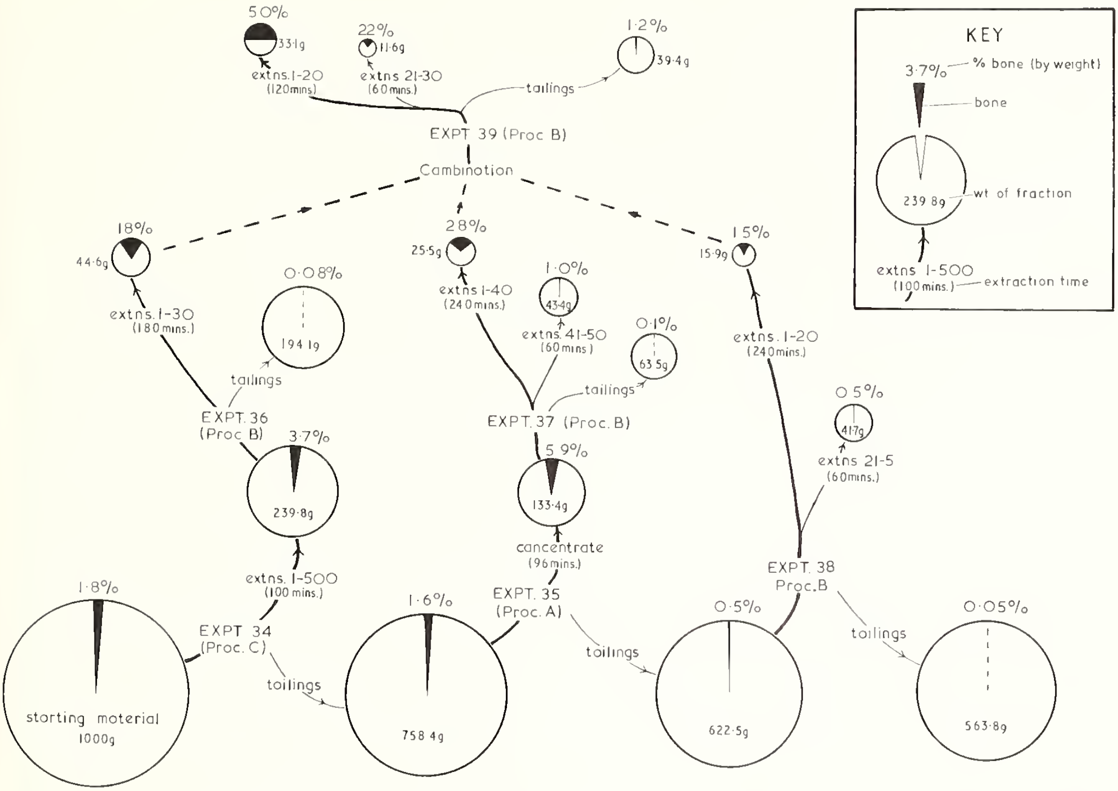
STARTING MATERIAL:– 5·00g of ?Telham Bone Bed, 0·5–1·0mm fraction
containing 7·5% bone and 91·5% quartz

Expt. no.	VARIABLE	TAILINGS Wt.	TAILINGS % bone	CONCENTRATE Wt.	CONCENTRATE % bone	CONCENTRATE Recovery of bone
	CONTAINER:-					
26	50ml beaker	4·57g	2·3%	0·43g	16%	48%
25	250ml beaker	4·23g	2·5%	0·77g	21%	70%
27	1 litre beaker	4·37g	2·1%	0·63g	13%	59%
	SOLVENT:-					
28	toluene	3·41g	3·2%	1·59g	8·5%	63%
29	xylene	3·48g	6·1%	1·52g	7·9%	40%
30	tetrachloroethylene	0·08g	3·3%	4·92g	7·5%	99%
31	chloroform	0·00g		5·00g	7·5%	100%
32	petrol	0·00g		5·00g	7·5%	100%
33	corn oil	0·00g		5·00g	7·5%	100%

Experiment 25 was also repeated with the paraffin being replaced by equal volumes of other organic liquids of widely varying physical properties, notably viscosity and density. Surprisingly, with the doubtful exceptions of toluene and xylene, none of these other liquids separated bone from the gangue particles (see Experiments 28–33).

SCALED-UP 'INTERFACIAL METHOD' SEPARATIONS

The techniques used in the small-scale experiments described earlier have been modified to make them more applicable to a scale large enough to be of practical use to the palaeontologist. I can see no reason why these scaled-up variants could not themselves be further scaled-up as desired, and without limit.



TEXT-FIG. 2. A large-scale separation of bone from quartz-rich sediment residue using the Interfacial Method. The starting material represented the 0·7–0·85 mm residue from 31·9 kg of the Cliff End Bone Bed. The areas of each circle and of the black sector within it are proportional to the weights of the fraction concerned, and of the bone therein, respectively. Abbreviations: Expt., Experiment; extns., extractions; Proc., Procedure; mins., minutes. For details of Experiments 34, 35, and 38, please see the text.

To sum up, in the experiments described in this section 1000 g of quartz-rich sediment residue, containing 1·8 % by weight of bone, was separated into 33·1 g of concentrate with 50 % of bone, 11·6 g of concentrate with 22 % of bone and 945·9 g of various residues containing between 1·2 and *c*. 0·05 % of bone. Details of the scaled-up procedures are given below, while the results are presented pictorially in text-fig. 2.

Scaled-up Procedure C (*Experiment 34*)

This was employed only once, as follows: 1000 g of well-washed 0·7–0·85 mm residue from 31·9 kg of the Cliff End Bone Bed was divided into two equal portions, each being placed in a 1 litre 'Pyrex' beaker. Domestic paraffin, 300 ml, and cold tap-water, 250 ml, were added to one of the beakers, and gently agitated; after settling, the water/paraffin mixture was decanted through a 0·5 mm sieve into the other beaker. This decantation process from one beaker to the other was repeated for a total of 500 times over a period of 100 minutes. During each of these 500 extractions, the interface between the paraffin and the water held a small quantity of material slightly enriched in bone, which accumulated on the sieve as 239·8 g of concentrate. For further details see text-fig. 2.

Scaled-up Procedure A (*Experiment 35*)

This too was employed only once, as follows. The 758·4 g of the tailings from Experiment 34 was placed in a square tin of side 23 cm and height 10 cm, along with 76 ml of tetrachloroethylene and 760 ml of a 1 % solution of 'Fairy Liquid' in cold tap-water. Small pieces of foamed polystyrene sheet (cut from 'takeaway' hamburger boxes) were added, and the mixture agitated gently. Pieces of the polystyrene were removed as and when they had acquired a coating of material enriched in bone, and were replaced with fresh polystyrene. This process was continued until the increasingly poorer yield and lengthening extraction times made further extraction unprofitable; in total it took 96 minutes and used 225 pieces of polystyrene with an estimated surface area of 9000 cm^2.

After removal from the tin, each piece of polystyrene was rinsed in cold water to remove non-adherent material not significantly enriched in bone, and was then dissolved in chloroform to allow the recovery of the concentrate. In total, 133·4 g of concentrate, containing 5·9% by weight of bone, was recovered (for further details see text-fig. 2).

Scaled-up Procedure B

The excellent results obtained with this procedure rapidly made it the 'workhorse' of this exercise, and it was used for all four of the remaining experiments. The most impressive of these (Experiment 38) is described below.

The 622·5 g of the tailings from Experiment 35 was placed back in the square tin used earlier, and wetted with 12·4 ml of domestic paraffin and enough 1% 'Fairy Liquid' solution to cover it to a depth of *c.* 5 mm (311 ml). Paraffin wax, recovered from earlier experiments and weighing 213 g, was melted in hot water and cast into thin flakes by pouring on to aluminium foil. One-fifth of these flakes were added to the tin, and the mixture gently agitated. Material enriched in bone slowly accumulated on the floating paraffin wax flakes, which were removed from the tin after 12 minutes agitation. Another four such extractions were then performed using the rest of the paraffin wax flakes, and with a fresh 12·4 ml of domestic paraffin being added to the tin before each extraction. When these had been completed, the paraffin wax was melted in hot water (containing a little detergent) to recover both the concentrate, which sank to the bottom of the hot water, and the paraffin wax, which floated on the surface. The molten paraffin wax was cast into flakes on aluminium foil and used in the next five extractions.

In all, twenty-five extractions were carried out as described above, the paraffin wax being recovered and recycled after every five extractions. The aqueous phase in the tin was replenished as necessary to compensate for losses. Similarly, fresh 12·4 ml aliquots of paraffin were added before each of extractions 1–11, 16, and 21, the spacing of the additions being as judged necessary to maintain both the quality and the quantity of the concentrates at a satisfactory level.

The first twenty extractions yielded 15·9 g of concentrate containing 15% of bone; as the starting material of the experiment contained only 0·5% of bone, this represents an enrichment of about thirtyfold. Other results from the experiment are shown in text-fig. 2.

In addition to its excellent performance, the scaled-up Procedure B described offers considerable economic advantages, due in large measure to the ease with which its most expensive component, the paraffin wax, can be recycled for reuse. As an example may be cited the paraffin wax used in the above experiment, which was originally obtained by melting domestic candles and which then weighed 383 g. It was used in all four of the scaled-up Procedure B experiments of text-fig. 2 and in another two experiments (not reported), during the course of which it was recycled twenty-two times. After this, it weighed 135 g and was still of suitable quality to be used again, if this had been necessary. Indeed, if anything, its effectiveness as a 'substrate' material had been improved by its being softened by the paraffin it had imbibed, which facilitated the adhesion of bone particles.

CLOSING REMARKS

How does the Interfacial Method stand at present? Even in its present embryonic form, the Interfacial Method is exceptionally useful in the recovery of microvertebrate fossils from sediment residues. It is effective over a wide range of gangue types and particle sizes, and with sediment residues containing both high and low concentrations of fossil bone. As a result, by multi-stage extractions one should be able to obtain high-grade bone concentrates from a wide range of poorly fossiliferous starting materials. The various embodiments of the Interfacial Method are all of very low operating cost, both in terms of money and manpower. Whilst subject to a variety of poorly understood variables, the Interfacial Method seems basically to be resilient in this regard, very few of the experiments that have been performed being total failures in the sense that no separation of bone from gangue minerals occurred at all. As further evidence of this fundamental resilience, the three embodiments described in this account (Procedures A, B, and C) use widely different materials and working procedures.

How could the Interfacial Method be further developed? The most exciting development would be a machine for the large-scale separation of bone from sediment residues; this should be possible by mechanization of Procedure C, whose simplicity and low cost makes it ideal for the purpose. Apart from this, the work described in this account needs to be consolidated, and in particular, the applicability of Procedures B and C to a comprehensive range of gangue types and particle sizes awaits study. Although residues finer than 0·35 mm have not yet been investigated, I anticipate that the Interfacial Method will prove especially useful in the recovery of conodonts and probably of phosphatized invertebrate microfossils. Other working procedures and 'solvent'/'substrate' systems also need to be investigated, for example, could paint films be useful 'substrates' with certain 'solvent' systems? The possibilities are endless.

On a more speculative level, perhaps the phenomenon on which the Interfacial Method is founded occurs in nature, and has played a part in the formation of certain kinds of bone bed, particularly those associated with bituminous sediments.

What will be the significance of the Interfacial Method for vertebrate palaeontology? Even now the Interfacial Method should enable comprehensive microvertebrate faunas to be obtained from sediments where they are at present either unknown, or are in terms of time and money, largely inaccessible to the collector. This in its turn should lead to an increased knowledge of certain obscure groups, notably Mesozoic mammals, and give a stimulus to the growing field of vertebrate palaeoecology by allowing faunal lists to be more frequently established on a quantitative basis.

But perhaps the single most important consequence of the Interfacial Method will be sociological. Up to now, microvertebrate fossils have been collected mainly by professional workers based in Europe and North America, who have been the only ones with the financial and manpower resources necessary when using earlier methods. The Interfacial Method will not only greatly assist these workers, but hopefully will also lead to a large increase in the number of active collectors, notably in countries where the resources available for palaeontology are small. It is also ideally suited to the amateur collector. This increase in manpower should lead to a corresponding increase in the number of productive localities and in their stratigraphic and geographic distribution. This, of course, will greatly enlarge the amount of fossil material available to the palaeontologist. When fully developed and widely applied, the Interfacial Method should have a highly stimulating effect upon vertebrate palaeontology.

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A NEW ACTINOPTERYGIAN FISH FROM THE MISSISSIPPIAN BEAR GULCH LIMESTONE OF MONTANA

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ABSTRACT. A new genus and species of tarrasiiform fish is described from the Chesterian (Upper Mississippian) Bear Gulch Limestone member of the Heath Formation, Montana, U.S.A. Among the distinguishing osteological features of the order that can now be established are premaxillae sutured in the midline, separate rostral and postrostral bones, two pairs of nasals, and a skull roof consisting of paired frontals, parietals, and postparietals. A tentative relationship is proposed with the base of the radiation of the order Palaeonisciformes.

TRAQUAIR (1881) named a most enigmatic fish from the Viséan Upper Border Group of Glencartholm, Dumfriesshire, Scotland (Lumsden *et al.* 1967), *Tarrasius problematicus*, a singularly appropriate specific name. Moy-Thomas redescribed this unique actinopterygian twice in four years (1934; Moy-Thomas and Dyne 1938) on the basis of additional but still inadequate material. It has been redescribed a third time by Jessen (1973), still without clarifying many cranial details and together with a new taxon from the German lower Upper Devonian, *Holopterygius nudus*. Jessen justifiably felt that the two species were somehow related through the common possession of a similar bladelike body form and continuous median fin, but was able to find no tangible characters linking *Holopterygius* definitively to any osteichthyan subclass.

The marine fish fauna of the Namurian Bear Gulch Limestone of Montana contains several specimens of two species belonging in the order Tarrasiiformes; one of these, described below, forms the basis of this report, while the other, far more specialized, fish will be dealt with in a subsequent paper. The osteology of the Bear Gulch tarrasiid described below reinforces as well as details the peculiar nature of this group as suggested by the previously known species. The known Tarrasiiformes are representatives of an adaptive radiation partaking of features that may have stemmed from near the origin of the Actinopterygii, and as such may have significance for interpretations of the interrelationships of the Osteichthyes.

The geological and ecological aspects of the Bear Gulch Limestone have been described elsewhere (Horner, in press; Horner and Lund, in press; DiCanzio, in press; Lowney, in press; Lund, Lund and Klein, in press; Lund, in press). In summary, however, the Bear Gulch limestone member of the Heath Formation was deposited in a small, shallow tropical bay. The water and superficial bottom sediments were well oxygenated, bottom sediments were very fine with relatively high but cyclically variable silica content (Williams 1979), deposition was quite rapid and there was no significant sessile benthic invertebrate community. Substrate for the fauna consisted of various sponges (Rigby, in press) and algae. Malacostracan crustaceans and several phyla of worms are among the more dominant aspects of the invertebrate fauna (Schram and Horner 1978; Schram 1979). There are approximately seventy species of fish currently known, including five species of coelacanths (Lund and Lund, in press), possibly two crossopterygians known from scales (Andrews, pers. comm.), about thirty-five chondrichthyan species (Lund, in press), and one acanthodian (Zidek 1980); the remaining species are actinopterygian (Lowney 1980). All but about eight species are known from holomorphs.

Specimens range in condition of preservation from scattered to excellent, although generally lacking three-dimensionality. The Tarrasiiformes, however, frequently preserve with somewhat

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three-dimensional skulls and axial elements. The matrix, while technically a limestone, is not appropriate for acid preparation, and specimens are generally prepared with fine needles. The bones of some specimens or regions of specimens are sacrificed for the preparation of latex peels (Baird 1955), while in other cases the bones may be viewed through liquids, either water, alcohol, or benzene, to determine bone growth zones and the paths of the calcite filled lateral line canals. Drawings are prepared from photographic bases; photographic methods have been discussed elsewhere (Lund 1980).

SYSTEMATIC PALAEONTOLOGY

Order TARRASIIFORMES

Diagnosis. Elongate bony fishes lacking pelvic fins, and with unpaired fins continuous from near the occiput to the anus. Pectoral fins lobed, supported by few, elongate radials. Squamation may be variously reduced or absent. The bones of the skull include paired premaxillae, a rostral and separate postrostral, one or more pairs of nasals, plus frontals, parietals, and postparietals, flanked posterolaterally by supratemporals and tabulars (pterotics). A dermosphenotic is present. Cheek bones may include scales not tightly associated into a plate, plus preoperculum and a prespiracular series, or may be reduced. The operculum is small, the suboperculum is similar to the numerous branchiostegals, the more anterior of which are elongated to resemble lateral gulars. The shoulder girdle is covered by the branchiostegals and suboperculum. The ventral end of the cleithrum is overlapped anteriorly by the long thin dorsal stem of the clavicle. The braincase is composed of several ossifications.

Genus PARATARRASIUS, new genus

Diagnosis. The genus is distinguished from other members of the order by the long maxilla with a rectangular cheek expansion, a complete squamation, a downturned tail and low anterior anal fin.

Type species. Paratarrasius hibbardi, new species.

Etymology. Para, close to; and *Tarrasius.*

Paratarrasius hibbardi, new species

Text-figs. 1–3. Plate 50, figs. 1–5

Type specimen. University of Montana 5557, part and counterpart.

Referred specimens. University of Montana (MV) 2841, 2918, 3562, 3600, 5558, 6931, 7395. Carnegie Museum (CM) 27275, 27376, 30651, 30652, 30780, 35229–35232, 35544, 35601, 37539, 37540, 37598.

Horizon and locality. Upper Chesterian, Mississippian (Namurian E2B; Lower Carboniferous) Bear Gulch Limestone member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana.

Diagnosis. Tarrasioid fishes ranging in length to 136 mm; the maximum head length/total length ratio is 0·155; maximum body height total/length ratio is 0·172; the total length/snout-vent length ratio is 1·746. There are 27 to 29 precaudal vertebral arches and 68 to 73 precaudal scale rows. There are 28 to 31 scale rows above the lateral line at the anal notch and 50 to 54 rows below the lateral line. There are 27 to 28 caudal vertebral arches, disappearing at the downturn of the tail, and 78 to 81 caudal scale rows. There are approximately 4 jointed, unbranched fin rays to each vertebral arch.

Etymology. Named in honour of the late Professor Claude W. Hibbard.

DESCRIPTION

Body form. The head is approximately $\frac{2}{13}$ of the total length, with a subterminal mouth. The body is bladelike, achieving maximum height just anterior to the anal notch, from which point the dorsal margin gradually declines (Pl. 50, fig. 1). The posterior end of the tail is downturned. The dorsal fin arises behind the head, achieves maximum height relative to the dorsal body outline until shortly before the ventral downturn of the axis, and then approaches the axis more closely. The fin is continuous around the posterior tip of the axis in the midventral line, appearing to end somewhat anterior to the downturned axis but continuing forward on the ventral surface as very small fin rays to the rear margin of the anal notch. Pelvic fins are lacking. Pectoral fins are borne upon scaled lobes, about half of the body height above the ventral midline (text-fig. 2). Squamation is relatively uniform, without specialized middorsal, ventral, or anal scales, although each scale in the lateral line is perforated for a pore. The first scale row behind the cleithrum is somewhat elongated. The first 8 to 9 ventral scale rows behind the cleithrum and clavicle follow the curvature of these elements; succeeding ventral scale rows assume the same anterodorsal linearity as is typical for all flank scales. Scale rows immediately below the dorsal fin and above the anal fin consist of smaller scales and change direction to approach the vertical. This involves 6 to 9 vertical scale rows dorsally in the trunk and ventrally in the caudal region, and 13 scale rows along the dorsal margin of the caudal region (Pl. 50, fig. 5; text-fig. 3). This is interpreted to mean that the base of the median fin was borne upon a narrow, scaled extension from the somewhat more rounded body outline.

The lateral line of the body extends parallel to the axis to the point of sharp downturn, whereupon it takes a very sharp ventral bend and ends (text-fig. 3). It, therefore, does not extend into the ventral downturn. In all other well-preserved Bear Gulch actinopterygians, the lateral line extends only a short way up the dorsal lobe, and turns sharply to end at or near termination of hypochordal fin rays, or the change from regular hypochordal rays to the fin rays of the caudal flap or terminal tuft (DiCanzio, in press; Lowney 1980). We feel that, given this landmark, the downturned axis of *Paratarrasius* is actually the anatomical homologue of the upturned axis and terminal lobe of other chondrosteans. The principle webbed median fin itself therefore would represent a fusion of dorsal fin, terminal tuft, and hypochordal caudal, the anal fin being represented only by very short rays extending to the anal notch.

The blade-like body form of *Paratarrasius* is found among many recent teleostean fish that inhabit extremely sheltered, weedy environments. Propulsion is generally by continuous undulation of the median fin, with attitudinal adjustments performed by the pectoral fins. Thrust of the median dorsal particularly can generate either forward or backward motion, dependent upon the direction of wave propagation. Propulsion is thus extremely slow, with escape acceleration being provided by few strokes of the entire caudal region.

It is virtually axiomatic that all recent fishes with this particular body form and propulsive system are also weak, active low frequency electroreceptors (Bullock 1973). This unfortunately cannot be verified in extinct fish.

Cranial osteology. There are two types of ornamentation found on the head of *Paratarrasius*, the first being fine closely spaced ridges paralleling the long axis of the fish, as found on the maxilla, the lower jaw, anterodorsal expansion of the preoperculum, and the 'antorbital'. The second type, which evidently succeeds the first during ontogeny, is a smooth, glossy complete surficial covering, broken only by rows of fine nutrient foramina that are found uniformly distributed across many bones, particularly of the skull roof. Smaller specimens show that the nutrient foramina are related to the spaces between ridges of primary ornamentation on bones such as the premaxillae, and cannot be considered to be pores as found in cosmine-bearing fishes. The growth of the secondary ornamentation has the profoundest effects upon the apparent osteology of the skull roof, for it completely obliterates sutures along the dorsal midline by about 115 mm in total length (Pl. 50, figs. 2, 4). Transverse sutures, as between tabulars and postparietals, do not seem to be affected. Further, the secondary ornamentation only seems to be present, within the size range of the available specimens, upon the bones of the skull roof and rostrum. Bones of the lateral surface of the head are not affected.

The premaxillae are small, initially paired, and meet in the midline, where they fuse by ornamental overgrowth. They are dorsally overlapped by the median rostral element in loose association, and bear a strong internal shelf near their anatomically ventral but posterior edge. A single row of fluted teeth is borne upon this shelf, the teeth thus facing posteroventrally and spanning the small space between the anterior ends of the maxillae. The rostral is about the same size as the fused premaxillae, also covered with glossy ornament, and carries the ethmoid commissure across the midline without evident pores. It is notched dorsally for the reception of the anterior edge of the postrostral.

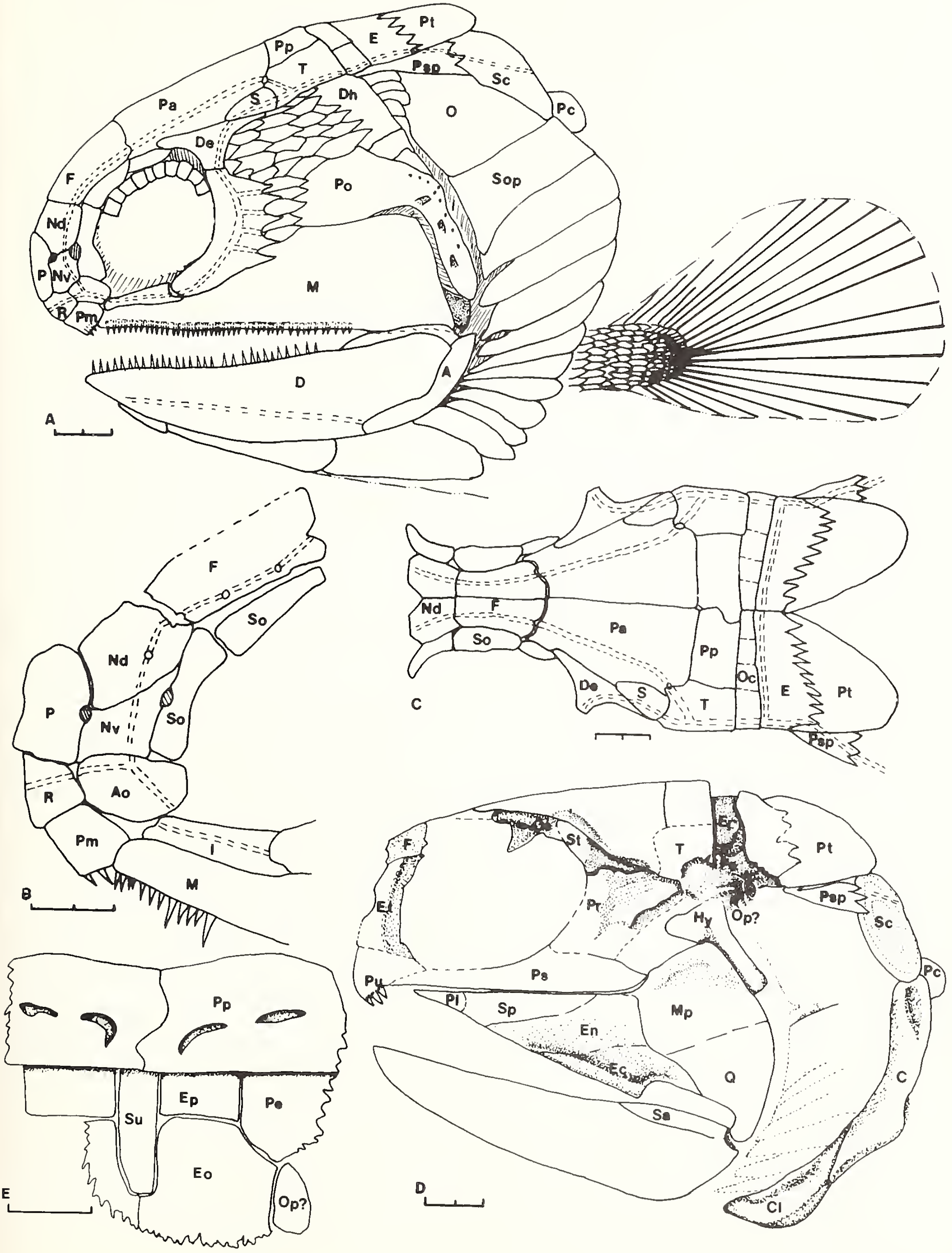
The single large postrostral has a glossy ornament. It is bordered laterally by two serial nasal bones on each side, and is notched midlaterally for the anterior naris. The anterior nasal element is somewhat expanded anteromesially, the posterior nasals meet in the midline posterior to the postrostral, and the nares seem to be represented by lateral notches at or near the common border of the two nasals. While the lateral line canal can be seen to traverse the middle of each nasal, its relationship to the ethmoid commissure cannot be precisely determined. There are few pores for the lateral line canal. The two nasals are bordered by a single long, angled supraorbital bone.

The frontals are initially paired but fuse across the midline to form a single element dorsal to the orbit. Prominent ventral flanges project from the lateral edges of the frontal (text-fig. 1*d*). The frontal bears the supraorbital canal near its lateral edges, and shows only few, tiny, regular pores associated with the canal (text-fig. 1*b*). The frontal meets the parietals in a conspicuous suture posteriorly, and is bordered laterally by a single supraorbital element. The parietals also fuse across the midline, forming the largest bone of the skull roof. It is notched laterally for the dermosphenotic anteriorly and for the supratemporal more posteriorly and is flanked laterally anterior to the dermosphenotics by a small supraorbital. The supraorbital lateral line canal traverses the parietal to enter the tabular at the posterolateral corners, in contrast to virtually every known bony fish. A few fine, irregular pores mark the path of the supraorbital canals across the parietal, but a large pore can be seen at the parietal-supratemporal-tabular junction (text-fig. 1*c*). There seems to be no communication via a transverse supraorbital commissure (Lowney 1980; Lund and Lund, in press) with the otic canal. The supratemporals are narrow, and receive the infraorbital canals from the loose dermosphenotics. The canals continue posteriorly as the otic canals into the small, almost square tabulars. The postparietals are mesial to the tabulars and bear two discontinuous segments of a transverse pit line almost to the mid-dorsal line (Pl. 50, fig. 2; text-fig. 1*e*). The suture between postparietals is sinuous and is not generally obscured by ornamental overgrowth. The supraoccipital ossification of the braincase does not participate in the skull roof.

At least two pairs of thin, small scale-like bones closely adhere to the posterior margin of the skull roof, followed posteriorly by the paired extrascapulars and post-temporals. The otic canal passes into the extrascapulars laterally, whence the occipital commissure passes mesially. From the extrascapulars the head canal passes into the lateral edge of the post-temporals, then posteroventrally into the bone called the post-spiracular in actinopterygians (Gardiner 1963; Lowney 1980).

The antorbital bone is rectangular in shape, ornamented with prominent horizontal ridges, and abuts against the rostral anteriorly, the anterior nasal anterodorsally, and the infraorbital posteriorly. It carries the infraorbital canal to the ethmoid commissure. While it appears most likely from the shapes of the bones and what is preserved of the paths of the lateral line canals that the nasal branch of the supraorbital canal (anterolateral commissure of Jarvik 1948; Stensiö 1947) joins the infraorbital canal at the antorbital, the precise position of this junction cannot be found. The infraorbital below the orbit is a strong ossification, tapering anteriorly, always tightly associated with the anterior end of the maxilla, and fitted through a curved suture to the posterior infraorbital. The latter element occupies the posteroventral quadrant of the superficial rim of the orbit, has a distinct mesially directed lamina, and usually bears fine strong, well-spaced posteriorly directed spikes along the posterior border. Occasional specimens reveal an irregularity of spacing, and one specimen bears six spikes, the dorsalmost two of which are thin and closely spaced. The infraorbital canal gives off short posterior branches that emerges to pores between the bases of the well-spaced spikes. The ventralmost two spikes are at the level of the anterior edge of the cheek expansion of the maxilla, and all spikes usually overlap the first row of cheek scales. The dermosphenotic is a strongly ossified Y-shaped element with a short ventral stem that carries the postorbital continuation of the infraorbital canal on to the skull roof.

TEXT-FIG. 1. *Paratarrasius hibbardi*, cranial bones. *a*, restoration of the external bones of the head. Based upon CM 35232, and MV 2841 and 5557. Scale in mm. *b*, partial restoration of the antorbital region of CM 35232. Scale in mm. *c*, restoration of the skull roof in dorsal view. Based on CM 35232 and CM 30583, and CM 27376, 35231, and 35544. Scale in mm. *d*, braincase, palate, and shoulder girdle in lateral view. Braincase and palate based on CM 35232. Scale in mm. *e*, braincase in occipital view, of CM 27376. Scale in mm. Abbreviations: A, angular; Ao, antorbital; C, cleithrum; Cl, clavicle; D, dentary; De, dermosphenotic; Dh, dermohyal; E, extrascapular; Ec, ectopterygoid; En, endopterygoid; Eo, exoccipital; Ep, epiotic; Et, ethmoid; F, frontal; Hy, hyomandibular; I, infraorbital; M, maxilla; Mp, metapterygoid; Nd, dorsal (posterior) nasal; Nv, ventral (anterior) nasal; O, operculum; Oc, occipitals; Op?, opisthotic?; Os, Orbitosphenoid; P, postrostral; Pa, parietal; Pc, postcleithrum; Pe, pterotic; Pm, premaxilla; Po, preoperculum; Pp, postparietal; Pr, pro-otic; Ps, parasphenoid; Pso, postspiracular; S, supratemporal; Sa, surangular; Sc, supracleithrum; So, Supraorbital; Sop, suboperculum; Sp, Suprapterygoid; St, sphenotic; Su, supraoccipital; T, tabular.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The scales of the cheek are somewhat variable, but occur in five to six anteroposteriorly overlapping rows between the posterior infraorbital anteriorly and the preopercular elements posteriorly.

The maxilla has the appearance of those of more typical Paleozoic actinopterygians, with a narrow anterior portion and a broad, almost rectangular cheek expansion (Pl. 50, fig. 2; text-fig. 1*a*). The buccal edge of the maxilla does not curve downward posteriorly, however, nor does the posterior end of the maxilla seem to have a shearing occlusion with the dentary. Further, judging by postmortem displacements, the maxilla is not firmly held to the preoperculum. This should not be construed as implying that the maxilla was mobile. Teeth on the maxilla are pleurodont, borne internal to the ornamented ventral margin of the bone, and occur in a single series with relatively sharp crowns. They cannot be considered 'peglike', as has been described for *Tarrasius* (Moy-Thomas 1934; Jessen 1973). There are no pit lines on the maxilla.

The preoperculum of most specimens is a single bone with a narrow ventral limb carrying the preopercular canal posterior to the maxilla, and a relatively short anterodorsal expansion ornamented with radiating lines. There is a short horizontal pit line at the junction of the two portions of the preoperculum, and there may be either few, prominent pores or possibly a quadratojugal pit line vertically upon the ventral limb (Pl. 50, figs. 2–4; text-fig. 1*a*). One specimen, however (MV 3600), has a preopercular of two separate ossifications, an anterodorsal and a posterior element each with distinctively different ornamentation (Pl. 50, fig. 3). In both cases, the preopercular canal occupies the posterior edge of the preoperculum, exiting through fine pores, and is not continuous to the anterodorsal part of the preoperculum, nor to the main head canal. The posterior and posterodorsal margins of the preoperculum are strongly associated with the same margins of the palate mesially.

The elements known variously as bone X or the dermohyals are a series of from one to four elements posterior to and parallel with the posterodorsal margin of the preoperculum, from the angle of that bone to the skull roof. They are strong elements, overlapped anteriorly by the last scale row of the cheek, and overlying, but not fixed to, the hyomandibular. There are several small scales between the posterior edge of the dermohyal series and the operculum (Pl. 50, figs. 2, 3; text-fig. 1*a*). These elements occur in the position of the prespiracular bone of coelacanths (Lund and Lund, in press) and the dorsal preoperculum of some Bear Gulch Actinopterygii, and a clear case has been made by Lowney (1980; in press) that they are related to the spiracular operculum.

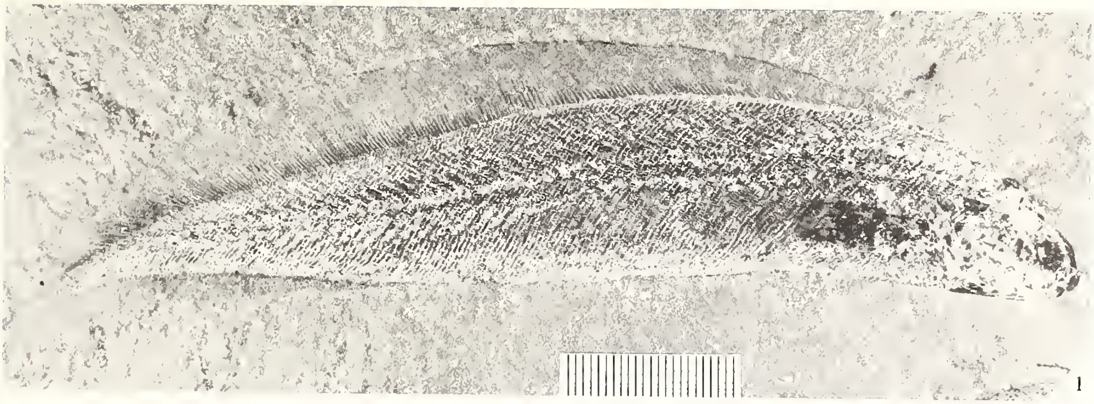
There are about fourteen bones in the opercular–branchiostegal series. The operculum is small and triangular. The suboperculum is slightly expanded anteriorly, is considerably longer and narrower than the operculum, and in appearance is continuous with the branchiostegals. The first and second branchiostegals are the longest of the series; there are three branchiostegals to the ventral end of the preoperculum. The fourth through tenth are progressively shorter, posterior to the lower jaw, while the eleventh is broad and elongate, underlying the posterior half of the lower jaw. Branchiostegals 12, 13, and 14 are narrow and almost as long as the lower jaw, while the fifteenth is short and there appears to be a very small median gular.

The articular of the lower jaw is elevated above the tooth row posteriorly (Pl. 50, fig. 3), as has been found in several other Paleozoic actinopterygians with a pleurodont maxilla (Heyler 1969; Lowney 1980). There is a long thin surangular dorsal to the rear margin of the dentary (Pl. 50, fig. 2; text-fig. 1*d*) and a thin angular along the rear of the jaw. The dentary is the principal bone of the lower jaw, and bears a thin band of tall, sharp teeth bucally.

What appear to be the sclerotic ossifications of *Paratarrasius* are peculiar among actinopterygians in being very numerous. Further, the dorsal elements are heavily ossified and slightly overlapping, while ventral elements have not been found. All are ornamented with faint lines. Normally, all actinopterygians are considered to have four sclerotics, while dipnoans and crossopterygians have numerous elements (Miles 1977). While Miles is inclined, justifiably, to dismiss the significance of sclerotic numbers in determination of ancestry the high number of sclerotics is one of the more outstanding different characters of this group of fish. Alternatively, these may not be sclerotics but a lateral supraorbital series as is found in primitive sarcopterygians (Lund and Lund, in press).

EXPLANATION OF PLATE 50

Figs. 1–5. *Paratarrasius hibbardi*. 1, type specimen, University of Montana (MV) 5557A. Scale in mm. 2, Carnegie Museum (CM) 35232A, latex peel of head. 3, MV 3600, latex peel of head. 4, CM 35544, latex peel of head. Arrow indicates hyomandibular. Scale in mm. 5, anterior caudal region of CM 30780A. Scale in mm.



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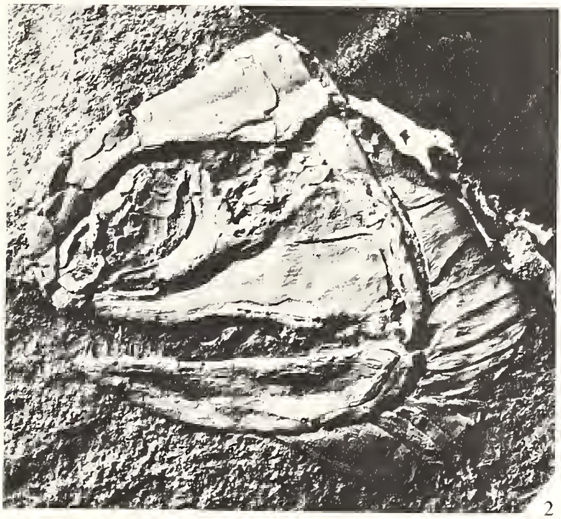

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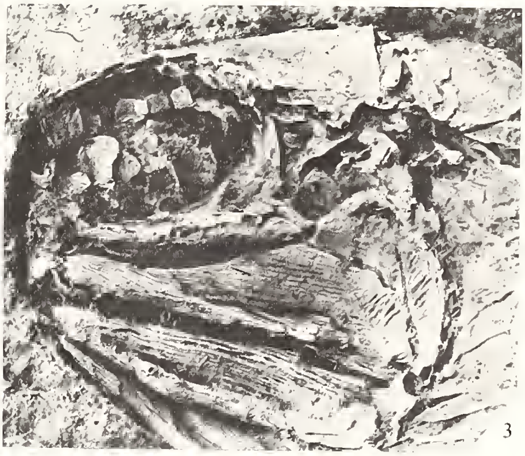

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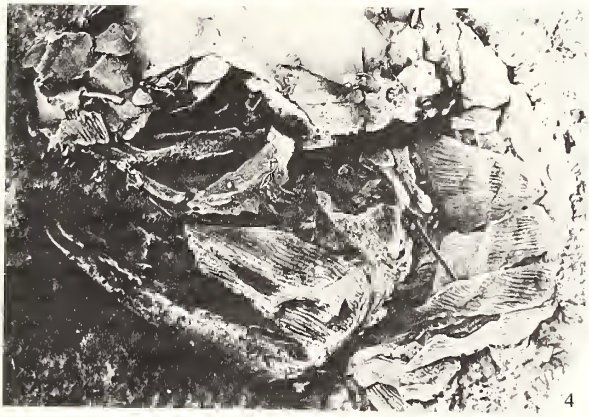

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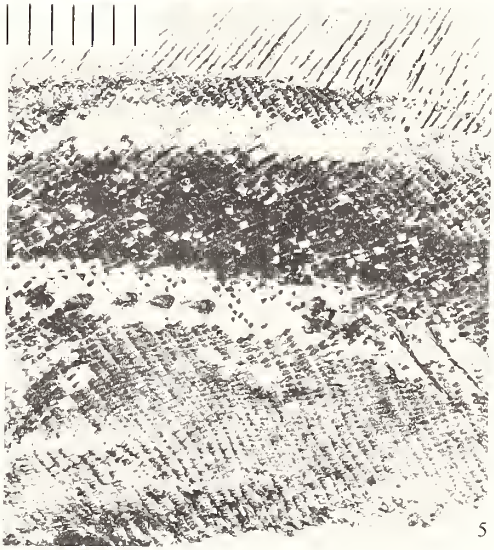


5

LUND and MELTON, *Paratarrasius*

The shoulder girdle of *Paratarrasius* consists of six paired bones in dorsoventral series, including the enlarged dorsal postcleithral scale (text-fig. 1*a* and *d*) a larger number of elements than has been described for any other osteichthyan (Rosen *et al.* 1981). The otic lateral line canal runs through only the anterolateral edge of the post-temporal, and through the next elements of the series, before entering the body scales. These elements have been termed the postspiracular and supracleithrum in standard actinopterygian nomenclature (Gardiner 1963; Lowney 1980). The postspiracular has been little noted in actinopterygian studies, and while it is commonly found, it has not previously been noticed either to carry the main lateral line nor to be an element of the shoulder girdle. The name itself is singularly inappropriate. The supracleithrum dorsally overlaps the end of the cleithrum and is ornamented with strong circumferential lines. The postcleithrum is scale-like in thickness, shape, and relationships.

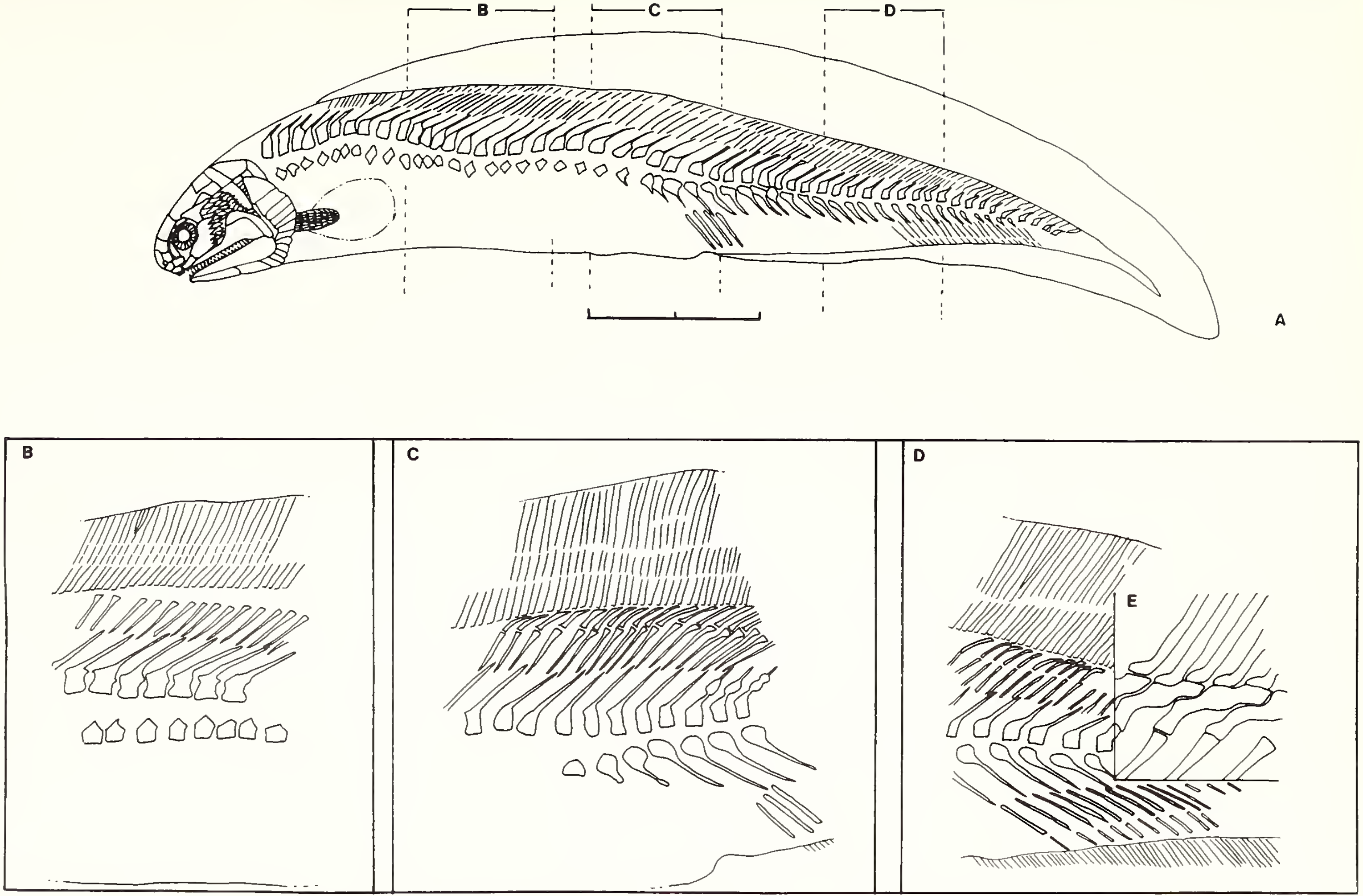
The cleithrum and clavicle are usually completely covered by the suboperculum and branchiostegal rays. They are well displayed only in CM 35231. The cleithrum is narrow and unornamented and ends immediately ventral to the base of the pectoral fin lobe. It is overlapped anteroventrally by the thin dorsal stem of the unornamented clavicle. There is no interclavicle; neither scapulocoracoid nor pectoral fin endoskeleton can be seen. Several problems of osteichthyan bone homologies and terminology are revealed by the tarrasiid shoulder girdle; these are discussed subsequently.

The palate is poorly displayed, and is known principally from MV 3600, CM 30780 and 35544 (text-fig. 1*d*). The palatine is very narrow, and bears a dermopalatine patch of strong, long, conical teeth. The endopterygoid appears to be long and thin, extending to about midway along the maxilla and bearing a single row of long teeth just mesial to a lateral flange contacting the maxilla. There is a thin dermal plate extending posteriorly from the endopterygoid that bears a fine shagreen of denticles. There may be a thin suprapterygoid plate along the mesial edge of the palate. The ectopterygoid continues the lateral margin of the palate, but has a strongly ossified, very marked opening for the adductor musculature between its posterolateral margin and the posteromesial end of the maxilla. The quadrate condyle is at the rear edge and only slightly below the ventral edge of this fontanelle. The metapterygoid is always almost completely covered by the preoperculum and seems to correspond with it in general outline; its posterior edge fits into a groove in the anterior edge of the short hyomandibular.

The hyomandibular is an extremely short element, obliquely articulated to the braincase with a double head at the level of the supratemporal–tabular suture and extending no further ventrally than the ventral end of the operculum (Pl. 50, fig. 4). Its contact with the palate is therefore limited to the posterodorsal edge of the metapterygoid. No other details of the hyoid arch can be resolved. The hyomandibular is essentially as illustrated by Jessen (1973) for *Tarrasius*.

The braincase is well ossified in several bones (text-fig. 1*d* and *e*). Anteriorly there is a strong ossification of the lateral wall of the ethmoid, suturing ventrally with the paired prevomers and parasphenoid. The prevomers meet in the midline and bear a prominent ventral platform upon which there are long teeth. The parasphenoid is extremely narrow in the orbital region, expanding under the braincase and apparently ending at about the level of the hyomandibular articulation. The parasphenoid bears fine granular teeth posteriorly. The lateral laminae of the parasphenoid are low, and there are no articulations between braincase and palate. The parasphenoid sutures posterodorsally with the pro-otic, and a sphenotic and small orbitosphenoid can be found (Pl. 50, fig. 3). Only a small corner of the hyomandibular facet may be borne upon the pro-otic, most of the anterior facet apparently being located upon the poorly displayed sphenotic ossification. There is a pterotic posterodorsally, although it cannot be determined whether it is co-ossified with the superficial tabular. The pterotic extends around to the posterodorsal edge of the occipital surface where it is excavated for a small post-temporal fossa (text-fig. 1*d*). There is a strong ridge, near the ventral margin of the lateral face of the pterotic, that usually marks the dorsal edge of a lateral temporal fossa in recent teleosts; this ridge is capped posteriorly by what appears to be an additional ossification in line with a ventral process of the post-temporal (text-fig. 1*d* and *e*) but further details are not available. The occipital surface slopes gently posteriad below the occipital or scale bones. On this shelf there is a narrow supraoccipital, in small part projecting between the dorsomedian ends of the exoccipitals. There is also a pair of epiotics lateral to the supraoccipital; the post-temporal fossa is small and open dorsally. The braincase, therefore, although incompletely known, is ossified in a number of parts that correspond roughly to the ossifications of the braincase of teleosts, rather than to the single unit found in Permotriassic actinopterygians (Obruchev 1967).

Axial skeleton. Neural arches are fused dorsally across the midline throughout the body, and are usually preserved in three dimensions. Neural spines are median and straight, and appear to be inserted into the dorsal ends of the neural arches. Ventral arch elements in the trunk are large and triangular. Haemal arches of the caudal region are essentially the same as the neural arches. Haemal spines are continuous with the



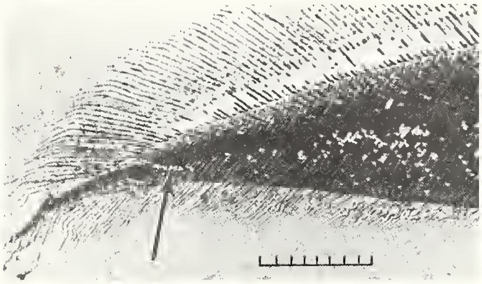
TEXT-FIG. 2. *Paratarrasius hibbardi*. *a*, axial skeleton. Based on MV 5557, plus. *b*, CM 37540. *c*, CM 30780. *d*, *e*, MC 5558, CM 37540.

arches in structure, and curve slightly posteriad distally as they taper to points. The first three or four haemal spines are closely associated with long, well-ossified epihaemals, apparently in 2:1 ratio to the spines. Only near the downturn of the caudal, where the ventral fin deepens, can there be seen two series of elements distal to the haemal spines (text-fig. 2*a*). There are no visible calcified centrum elements and no contact between neural and haemal arch elements.

Dorsally, each neural spine is closely associated with the ventral ends of two epineural rods, each of which, in the thoracic region, bears a small posterodorsal expansion with an articular facet for a more distal element (text-fig. 2*b* and *c*). These articulations are internal to the change in scale row orientation (Pl. 50, fig. 5). Each of the distal elements is straight anteriorly, and articulates with (usually) two fin rays. Each fin ray throughout the median fin bears an anterior process that almost contacts the fin ray next anterior. At the beginning of the caudal region the epineural-distal articulation enlarges and approaches the vertical, while the distal elements curve posteriorly and then dorsally to the bases of the fin rays (text-fig. 2*d* and *e*). At the level of the twelfth caudal segment, as the body taper becomes marked, the distal elements start becoming progressively shorter relative to the proximal segments and neural spines, where they can still be seen to be the only elements articulating with the fin rays. Neither axial nor peripheral elements are visible in the downturned caudal axis.

The two series of radials supporting the median fins may be primitive for Osteichthyes (Lund and Lund, in press), and may be homologized with axonosts and baseosts. We can find no basis, however, for Jessen's (1973) elaborate restoration of these structures in *Tarrasius*. As far as can be determined, the axial skeleton of *Tarrasius* differs principally in numbers of vertebral elements from that of *Paratarrasius*.

The anterior region of the peritoneal cavity often is preserved with a prominent black stain, in the position expected for a liver (Pl. 50, fig. 1).



TEXT-FIG. 3. *Paratarrasius hibbardi*, posterior caudal region of CM 30780 (arrow indicates the terminus of the lateral line canal). Scale in mm.

RELATIONSHIPS

Moy-Thomas's first (1934) description of the skull roof of *Tarrasius* was somewhat closer to the osteology of *Paratarrasius* than the second (Moy-Thomas and Dyne 1938). He originally described the large and unique frontals, and large supratemporal, subsequently changing the frontals to a large 'postrostral' and obliterating sutures he had, in reality, seen correctly in his original description. There is adequate reason to believe that with sufficient material the process of skull suture obliteration that characterizes both genera would have become clear to Moy-Thomas in *Tarrasius*. The cheek is poorly preserved, and the presence of cheek scales cannot be determined from the Glencartholm material. The maxilla is rounded posteriorly, however, and overlaps the posterior end of the lower jaw as in many other chondrostean-level actinopterygians; there is no clear evidence of pleurodonty and the teeth are called peg-like, marked differences with the Montana species. Both opercular and subopercular bones are larger, and branchiostegals are more numerous. Moy-Thomas illustrates eight elongate pectoral radials supporting the fin (Moy-Thomas 1934), an area which is obscure in *Paratarrasius*. Vertebral elements in the trunk of *Paratarrasius* are more numerous, and the median fin outlines differ dramatically, along with the termination of the body. It is not certain, however, to what degree these differences are caused by poor preservation. Again, preservational differences may account for Moy-Thomas's restoration of three rows of dorsal radials distal to the neural spines; Jessen (1973) illustrates an entirely different structure, and one for which we could find no basis in any specimens. *Tarrasius* lacks all but lateral line scales anterior to the caudal region. If this is simply representative of an early ontogenetic stage of scale development, in a pattern typical of acanthodians and many osteichthyans (Zidek 1976; Lowney 1980, 1980*a*), then scale development of *Tarrasius* is still significantly delayed relative to the condition in *Paratarrasius*. In *Paratarrasius* all specimens from less than 90 mm preserved length have complete squamation.

Holopterygius nudus is known from one specimen that basically agrees with other Tarrasiiformes in the body form, elimination of the pelvics, and in axial skeleton, all characters that are rather inadequate ones upon which to base relationships (Jessen 1973). There is, however, also striking agreement between the shoulder girdles of *H. nudus* and *P. hibbardi*. One can judge from the three forms that experimentation with scale reduction may have been a feature of the group. *H. nudus* has interarticulating arches, not seen in either of the other species, and has apparently singularly weakly ossified skull bones. These are all features characteristic of the undescribed Bear Gulch tarrasioid. It may be suggested that *Holopterygius* is more specialized, and less closely related to either *Tarrasius* or *Paratarrasius* than they are to each other.

There are several osteological features of *Tarrasius* and *Paratarrasius* that in combination are shared by no other known Paleozoic actinopterygian. These include the serial nasals, the presence of bones that can be called frontals, parietals, and postparietals, the supraorbital canal entering not the postparietals but the tabulars, the scale rows on the cheek, and the body and fin form. The dermal shoulder girdle, however, raises the most questions.

The dermal shoulder girdle of *Paratarrasius*, and of many Paleozoic actinopterygians, consists of six paired bones, the post-temporal, 'postspiracular', supracleithrum, postcleithrum, cleithrum, and clavicle. A median interclavicle is absent. The shoulder girdle of sarcopterygians seems to lack the 'postspiracular' anterolateral to the post-temporal-supracleithrum joint, and incorporates an anocleithrum between, and overlapped by, supracleithrum and cleithrum (Andrews and Westoll 1970, 1970*a*; Rosen *et al.* 1981). The anocleithrum has been considered to be homologous to the actinopterygian postcleithral scale on the basis of topographic location and overlap relationships (Rosen *et al.* 1981) while the inappropriately named postspiracular has not previously been observed to carry a lateral line canal or to be an element of the shoulder girdle.

The tarrasiid shoulder girdle suggests several possible alternative interpretations of the dorsal bones of the series. First, the tarrasiid arrangement of post-temporal, postspiracular, supracleithrum, and cleithrum-postcleithrum may be uniquely derived among the Paleozoic actinopterygians, a remote possibility in the light of the prevalence of this arrangement (Gardiner 1963; Lowney 1980). The lateral line canal traversing the postspiracular seems to be unique, however. Second, the arrangement may be primitive for the Actinopterygii and bone nomenclature and homologies are essentially correct among osteichthyan groups, in which case the condition may also be considered primitive relative to the Sarcopterygii. Third, the tarrasiid arrangement may be uniquely derived relative to the known sarcopterygian linkage with the post-temporal and braincase. Fourth, bone homologies may not be correct; the actinopterygian postspiracular being homologous to the sarcopterygian anocleithrum, and the postcleithrum not being an element of the shoulder girdle of primitive members of either group. Overlap and lateral line relationships between postspiracular and supracleithrum do not correspond to that of the sarcopterygian supracleithrum and anocleithrum, strongly suggesting that these homologies cannot be demonstrated. The absence of a distinct postcleithral shoulder girdle element either in *Mimia* (Rosen *et al.* 1981), in tarrasiids, or in other Paleozoic actinopterygians suggests that there is no convincing evidence for a proposed anocleithrum-postcleithrum homology. The weight of evidence suggests that either alternative two or three are the most acceptable; that this arrangement may be either primitive for actinopterygians or uniquely derived. A median interclavicle, absent in tarrasiids, is also lacking in primitive actinopterygians (Lowney 1980) and in primitive sarcopterygians (Lund and Lund, in press, contrary to Rosen *et al* 1981), and is not a useful character in known Paleozoic actinopterygians.

Patterns of ossification of the bones of the suborbital region of the cheeks of actinopterygians are highly variable with the weight of evidence indicating that either a disorganized or fully scaled region between the infraorbital series and the preopercular bones represents the primitive condition (Lowney, in press; 1980). Sarcopterygians as well show cheeks consisting of a large and variable number of cheek bones, although these are usually integrated into a cheek plate (Jarvik 1948; Westoll 1949). The sarcopterygian preopercular lateral line canal traverses a variable number of bones before contacting the jugal canal (Jarvik 1948; Westoll 1949); the suggestion that the single preopercular bone of tarrasiids is a derived condition relative to a large number of bones in series is reinforced by several Bear Gulch actinopterygians with two bones in the series (Lowney 1980).

The presence of a series of bones in the spiracular operculum may be regarded as a more primitive state than that of the single prespiracular bone of sarcopterygians (Lund and Lund, in press). In this case, more primitive conditions than that of the tarrasiids are known from other Bear Gulch Actinopterygii (Lund, manuscript; Lowney, in press), and no actinopterygian shows any indication of the submandibular series of certain sarcopterygians (Lund and Lund, in press). The presence of the dorsal portion of the mandibular operculum in Actinopterygii and the ventral portion of the mandibular operculum in Sarcopterygii is interpreted as reinforcing this subdivision of the Osteichthyes.

The rostral regions of sarcopterygians, where they are not fused into single solid blocks, are mosaics of many bones (Lund and Lund, in press). The rostral region of *Paratarrasius* consists of premaxillae meeting in the midline, a derived condition even among the actinopterygians; followed by a median rostral carrying the ethmoid commisure, a primitive character for the osteichthyans; followed by a separate postrostral (a derived character, several postrostrals seem to be primitive for the Osteichthyes); flanked laterally by two serial nasals, a primitive character for known Actinopterygii but derived relative to the sarcopterygian condition (Lowney 1980; Lund and Lund, in press). There is no actinopterygian that has been observed to have the 'bone' called the rostropremaxilloantorbital (Gardiner 1963, 1967) either primitively or otherwise (Lowney, in press; 1980). *Paratarrasius* and *Tarrasius* have an additional paired bone of the skull roof not found in other actinopterygians, here termed the frontals, a primitive character. This paired bone is bordered posteriorly by a conspicuous suture reminiscent of the intracranial joint of many crossopterygians, but the structure of the braincase and skull roof of *Paratarrasius* seems to preclude such a joint. In view of the gross differences of skull roofing bone patterns among the sarcopterygians (Andrews 1973; Lund and Lund, in press; Rosen *et al.* 1981) no reasonable homologies can be drawn between the tarrasiid 'frontals' and the bones of any known sarcopterygian.

It should be noted that while the occipital scale bones seem to be prevalent among Paleozoic actinopterygians, they have been little noticed in the literature (Lowney, pers. comm.). They clearly do not bear the extrascapular lateral line commisure, and their significance is not clear.

The median fin condition of two rows of serial radials supporting fin rays is shared by other actinopterygians and Dipnoi (Lowney 1980; Obruchev 1967). The endoskeleton of the pectoral fin of *Tarrasius* consists of a row of radials, again in primitive contrast to the single proximal element of the Sarcopterygii but consistent with other actinopterygians.

The Tarrasiiformes can clearly only be considered actinopterygians. Among these, however, they are primitive in retaining a separate rostral, two pairs of nasals, frontal bones, a supratemporal, scale rows on the cheek, and a portion of the spiracular operculum (Lowney 1980). Derived characters that may be useful in determining relationships include the premaxillae suturing across the midline, a Y-shaped dermosphenotic, the supraorbital canal extending into the tabular, reduction but not elimination of the supraorbital bones, a somewhat oblique articulation of the hyomandibular to the braincase, the lack of a quadratojugal bone and the presence of a single preopercular bone, pleurodont dentition on the maxilla, and reduced scale size with increased numbers of scale rows. The numerous branchiostegals may also constitute a derived condition.

Derived characters of the premaxillae and rostral along with numerous branchiostegals and reduced scales are shared with the order Palaeonisciformes, as restricted by Lowney (1980). Tarrasiiformes do not, however, share the marked palaeonisciform character trends of a strongly protruding rostrum, reduction of the suborbitals to two bones, extremely oblique suspensoriums, and reduction to elimination of the spiracular operculum.

There are a number of derived characters that the Tarrasiiformes share with a new order incorporating the Paramblypteridae, the Aeduellidae, and several Bear Gulch fish ('fatfish', 'deep belly'—Lowney, in press; Lowney 1980). These include the Y-shaped dermosphenotic, the reductions of the supraorbital series, the elevated articular and pleurodont maxilla, and, with aeduellids, the path of the supraorbital lateral line canal. The Tarrasiiformes also share a number of primitive characters in common with this group, such as the scaled cheek, the state of the spiracular operculum, and the retention of the supratemporal bone. They do not, however, share the most typical trends within this group, such as the tight premaxilla–antorbital association, the development of cervical vertebrae, and the presence of pseudocentra. Further, of the derived characters shared in common, all but perhaps the path of the supraorbital canal are characters known to have arisen independently among other Paleozoic actinopterygians. The supraorbital canal entering the tabular, further, is the only known derived character that the Aeduellidae and Tarrasiiformes share in common.

The Tarrasiiformes share no other derived characters with any other known actinopterygian. It must be tentatively concluded that this order may have diverged from the Palaeonisciformes, but close to the basal stock prior to the establishment of many of the more characteristic trends that distinguish the later members.

SUMMARY

The Tarrasiiformes incorporate a number of primitive characteristics not previously known among the Actinopterygii, such as the presence of distinct frontal bones, two pairs of nasals, and an additional canal-bearing bone in the shoulder girdle, the postspiracular. The available evidence seems to indicate a relationship with a basal stock of the order Palaeonisciformes.

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A PARABLASTOID FROM THE ARENIG OF SOUTH WALES

by C. R. C. PAUL *and* J. C. W. COPE

ABSTRACT. *Blastoidocrinus antecedens*, from the early Arenig Bolahaul Member of the Ogof Hên Formation at Llangynog, South Wales, is the oldest known parablastoid and the first recorded from the British Isles. It is characterized by almost smooth deltoids with weakly scalloped margins and a stellate thecal outline. A single deltoid is known from the Treiorwerth Formation (Upper Arenig) of Anglesey.

Currents in the respiratory cataspires of parablastoids entered the aboral slits and exited through the adambulacral pores, contrary to Hudson's (1915) interpretation. Cataspire canals deepened during growth by internal resorption and external resecretion within the thecal cavity. This wasteful mode of enlargement may have limited the success of the Parablastoidea.

ALL but one of the specimens described in this paper come from a small disused quarry near the village of Llangynog (some 8 km south-west of Carmarthen), South Wales, in which are exposed some 15 m of silty mudstones the lower 2·5 m of which have yielded an extraordinarily rich and diverse fauna. The basal beds of the quarry lie about 13 m above the highest exposed crags of a coarse conglomerate with clasts of vein quartz and rhyolite. The conglomerate is seen locally to overly Tremadoc rocks (Cope, Fortey and Owens 1978) and is identified with the Allt Cystanog Member of the Ogof Hên Formation described by Fortey and Owens (1978) to the east of Carmarthen. Overlying the Allt Cystanog Member is the Bolahaul Member (Fortey and Owens 1978, pp. 233–234) known from several places in the area to the south-west of Carmarthen (Cope 1979) and it is to this member of the Ogof Hên Formation that the beds in the quarry belong. Their early Arenig age is shown by the common occurrence of the trilobites *Merlinia murchisoniae* (Murchison) and *Neseuretus parvifrons* (M'Coy). In addition a single specimen of *Phyllograptus* aff. *angustifolius* Hall has been found (see Fortey and Owens, 1978, p. 288). At Llangynog the fauna also includes (in order of abundance) bivalves, brachiopods, nautiloids, gastropods, dendroids, hyolithids, conulariids, monoplacophorans, and a single rostroconch. Because of the importance of this fauna, which is seemingly confined to a single small quarry, precise details of the locality are not published here. Full details are, however, deposited with the parablastoid specimens in the register of the National Museum of Wales.

Except for two isolated deltoid plates, the Llangynog parablastoid specimens come from a single bed of bioturbated silty mudstone containing occasional vein quartz and rhyolite pebbles; the unit is 10–15 cm thick and lies some 1·5 m above the lowest horizon exposed in the quarry. This bed has yielded most elements of the fauna mentioned above, but fossils are not as abundant in it as in beds a little higher in the quarry. The other two deltoid plates come from an horizon approximately 1 m above the main parablastoid-yielding bed. Altogether almost 1 tonne of the parablastoid-yielding bed was collected and broken up in the laboratory to furnish the material on which this description is based. When all the available material was examined, it became clear that it belonged to the parablastoid genus *Blastoidocrinus* Billings, previously known from the Lower and Middle Ordovician of North America. The Welsh specimens differ in some respects from all previously described American forms and so are here described as a new species, *B. antecedens*.

Re-examination of a small collection of echinoderm fragments from the Upper Arenig Treiorwerth Formation of Anglesey, sent to CRCP by Dr. D. E. Bates in 1975 revealed a further isolated parablastoid deltoid (Pl. 51, fig. 9), which probably also belongs to *B. antecedens*.

[Palaeontology, Vol. 25, Part 3, 1982, pp. 499–507, pl. 51.]

Parablastoids, as the name implies, are primitive, stemmed echinoderms with a cup superficially similar to that of a blastoid, but which bears distinctive internal respiratory structures, called cataspires by Hudson (1915). Parablastoids have five recumbent ambulacra which extend down over the theca between five large deltoid plates. The deltoids support the cataspires internally. In *Blastoidocrinus* the base of the cup is composed of numerous rather small plates, while in *Meristoschisma* Sprinkle, there is a single circlet of radial plates, with minute basals within the hollow where the stem attaches to the theca. The base of the theca is poorly known in *Blastocystis* Jaekel, the third genus of parablastoids. The cataspires of parablastoids are similar to the hydrospires of true blastoids in being composed of internal canals, but they differ in being largely associated with a single plate, the deltoid. Each cataspire canal opens at one end in a small pore along the ambulacral margin of the deltoid and at the other in a slit along the aboral edge of the deltoid. In *Blastocystis* and *Blastoidocrinus* the aboral opening is a short slit, while in *Meristoschisma* it is a long slit, internally divided into a series of short slits by calcite ridges (see Sprinkle 1973, pls. 34–41). Sprinkle also pointed out that there is not necessarily a one to one relationship between the number of deltoid slits and adambulacral pores and hence that some cataspire canals must branch.

Hudson (1911, pp. 203 *et seq.*) deduced that sea water entered via the adambulacral pores and exited through the deltoid slits. He coined the term 'cataspires' (1915, p. 165) for these unique structures because he believed the flow was away from the mouth (i.e. aboral) in contrast to the adoral flow in true blastoid hydrospires (which Hudson termed anaspires).

Isolated deltoids, as well as the original internal mould, show that the new Welsh species possessed cataspires and is hence a parablastoid. One specimen shows the complex plating of the aboral theca while another reveals the ambulacral 'wing plates' (see below) which together characterize *Blastoidocrinus*.

SYSTEMATIC PALAEONTOLOGY

Class PARABLASTOIDEA Hudson 1907

Diagnosis. Stemmed blastozoan echinoderms with a blastoid-like cup, the oral surface of which is composed entirely of five recumbent ambulacra and five large deltoid plates. Each deltoid bears internal respiratory structures, called cataspires, which consist of a set of canals that open in pores along the ambulacral margins, and in slits along the aboral margin, of the deltoid.

Discussion. The cataspire system is unique to parablastoids and nothing quite like it is found in any other echinoderm group. Although cataspire canals are internal, thin, folded membranous structures like rhombiferan dichopores or blastoid hydrospires, unlike these structures they are largely associated with a single thecal plate, the deltoid. Both dichopores and hydrospires are almost equally developed in two adjacent plates.

Currently three genera are assigned to the class and they are most easily distinguished on their ambulacral and thecal structure. In *Meristoschisma*, the only genus of the family Meristoschismatidae, the ambulacra are relatively short and wide, taper rapidly away from the oral pole and the aboral portion of the theca is composed of five large radials and very small basals which lie entirely within the depression into which the stem inserts. In *Blastoidocrinus* the ambulacra are relatively long and narrow, scarcely taper at all so that their sides appear to be parallel, and each is surmounted by a blade-like structure composed of up to three 'wing plates' against which the brachioles rested in life. The aboral theca of *Blastoidocrinus* is complex and incorporates basals, radials, bibrachials, and interbrachials (see Hudson 1907, fig. 1, p. 99). The third genus, *Blastocystis*, is poorly known, but to judge from Schmidt's (1874) original figures, it has parallel-sided ambulacra without 'wing plates' and possibly large plates in the aboral theca. At present, *Blastoidocrinus* and *Blastocystis* are referred to the family Blastocystidae Jaekel, 1918. The two parablastoid families are most easily distinguished on the deltoids which have long slits (divided internally) for the cataspire canals in meristoschismatids, but a single short slit confined to the aboral margin of the deltoid in blastocystids. Thus even isolated deltoids may be assigned to their respective families. The new Welsh species has deltoids with aboral slits only, ambulacra with 'wing plates', and an aboral theca which includes radials and bibrachials. It is therefore referred to the genus *Blastoidocrinus*.

Family BLASTOCYSTIDAE Jaekel, 1918

Diagnosis. Parablastoids with parallel-sided ambulacra and deltoids with cataspire slits along the aboral margin only.

Genus BLASTOIDOCRINUS Billings, 1859

Type species. *Blastoidocrinus carchariaedens* Billings, 1859, by monotypy.

Diagnosis. A genus of Blastocystidae with ambulacra-bearing wing plates and the aboral theca composed of a large number of different plates.

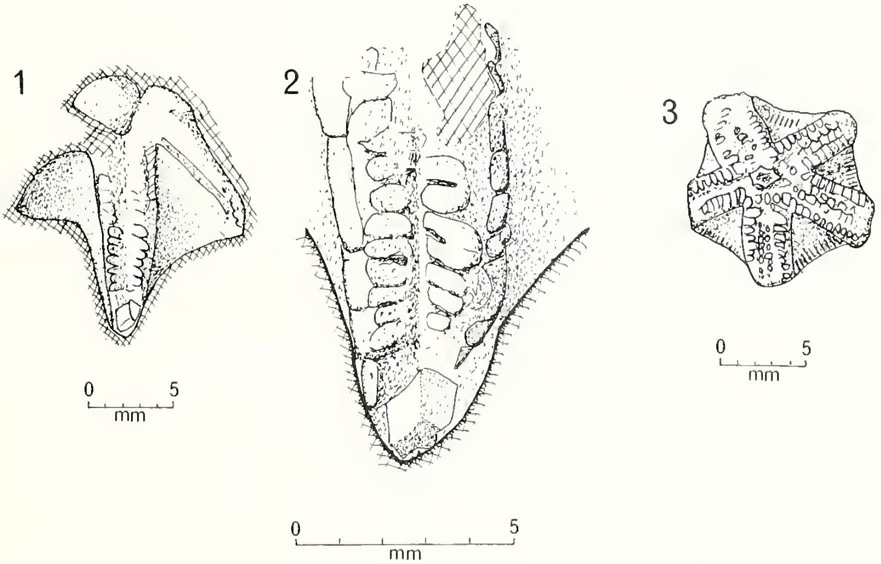
Blastoidocrinus antecedens sp. nov.

Plate 51; text-figs. 1–9

Diagnosis. A species of *Blastoidocrinus* with stellate thecal outline, almost smooth deltoids, and other thecal plates ornamented with only a few irregular ridges and grooves.

Types. Holotype (Pl. 51, fig. 2; text-fig. 3), National Museum of Wales, NMW 78. 8G. 1. Paratypes, National Museum of Wales, NMW 78. 8G. 2-34.

Material. Four partially complete or partially exposed thecae and thirty isolated deltoid plates.

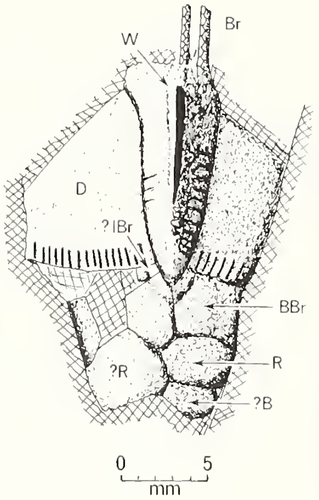


TEXT-FIGS. 1–3. Camera lucida drawings of *Blastoidocrinus antecedens* sp. nov. L. Arenig, Llangynog, South Wales. 1, paratype (NMW 78. 8G. 2) to show thecal outline and one ambulacrum which has lost the 'wing plates'. 2, detail of best preserved ambulacrum of the same specimen. 3, holotype (NMW 78. 8G. 1) to show stellate thecal outline. Matrix cross-hatched in figs. 1, 2.

Horizon and locality. Bolahaul member, Ogof Hên Formation (early Arenig), near Llangynog, South Wales, and Treiorwerth Formation (Bates, 1968) (Upper Arenig) Anglesey, North Wales.

Description. Stem (Pl. 51, fig. 1): associated with the specimens is a small fragment of stem, about 7·5 mm long by 3 mm maximum diameter and composed of 10 or 11 columnals. The columnals are circular in section, cylindrical, and smooth externally. Apparently they had a moderately large rounded lumen and the articulation surfaces lack radiating crenellae or any other ornament. It is by no means certain that this stem fragment belongs to *B. antecedens*, but its lack of external ornament suggests that it might originate from this species. The only other stem fragments appear to belong to a glyptocystitid cystoid.

Theca: pentagonal to star-shaped in outline (Pl. 51, fig. 3; text-figs. 1, 3). The best-preserved example (the holotype) is about 12 mm across. The five deltoids are identical, triangular in outline, and, in the holotype, 6 mm tall by 4 mm across the aboral suture. Each bears traces of nine to eleven cataspire canals. Larger isolated deltoids reach 16 by 12 mm and have up to twenty-two cataspire canals. Thus if thecal proportions do not change with growth, the theca must have reached 30–35 mm in diameter. Aborally, the theca has a pair of bibrachials radially beneath the tip of each ambulacrum and (probably) five radials which form a closed circlet beneath the bibrachials. From their size, the bibrachials do not surround the theca completely and we infer that interbrachials also existed, one of which is possibly preserved on one paratype (text-fig. 4).

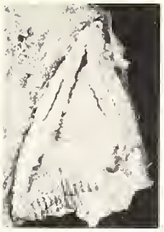


TEXT-FIG. 4. Paratype (NMW 78. 8G. 3) to show ambulacral 'wing' (w) and plates of the aboral theca. ?B, possible basal plate; BBr, bibrachial plates; Br, brachiole; D, deltoid; IBr, interbrachial plates; ?R & R, possible radial plates. Matrix cross hatched.

EXPLANATION OF PLATE 51

Figs. 1–13. *Blastoidocrinus antecedens* sp. nov. L. Arenig, Llangynog, South Wales and Treiorwerth Formation, Anglesey, North Wales. 1, latex of external surface of large isolated deltoid. NMW 78. 8G. 8, ×3. 2, latex of stellate plate that may represent the central plate of *B. antecedens*. NMW 78. 8G. 6, ×3. 3, stereophotos of Holotype, NMW 78. 8G. 1, ×4. 4, partial theca showing aboral surface of cup and one ambulacrum. NMW 78. 8G. 3, ×2·5. 5, stereophotos of latex of specimen in fig. 4 to show cup plating and ambulacral 'wing' (above). NMW 78. 8G. 3, ×2·5. 6, latex of internal surface of a small deltoid showing damaged cataspire folds. NMW 78. 8G. 7, ×3. 7, latex of external surface of almost smooth deltoid. NMW 78. 8G. 10, ×3. 8, stereophotos of internal surface of very large deltoid showing traces of cataspire folds. NMW 78. 8G. 5, ×3. 9, stereophotos of isolated deltoid from the Treiorwerth Formation, Anglesey. NMW 81. 11G. 1, ×3. 10, latex impression of stem fragment which possibly belongs to *B. antecedens*, NMW 78. 8G. 4, ×3. 11, latex impression of external surface of very large deltoid (counterpart to fig. 8). Note the cataspire slits (below). NMW 78. 8G. 5, ×3. 12, stereophotos of latex of partial theca showing one ambulacrum without 'wing plates'. NMW 78. 8G. 2, ×3. 13, latex impression of internal surface of one small deltoid of NMW 78. 8G. 3, ×3. All figures whitened with ammonium chloride sublimate.

PLATE 51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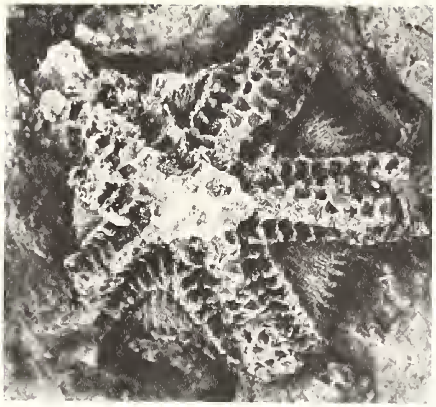
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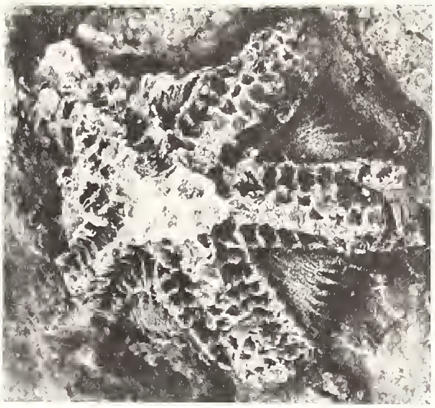

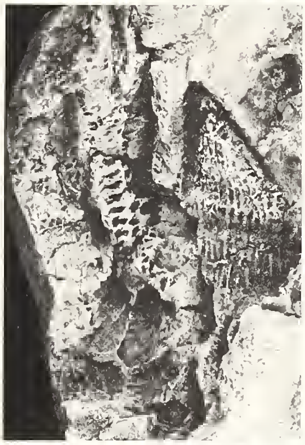
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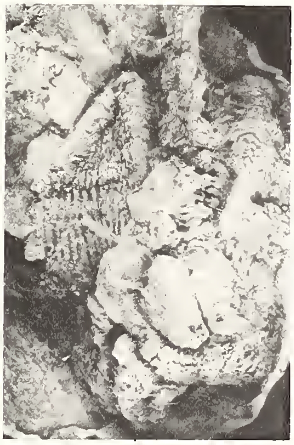
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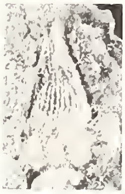
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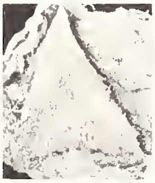
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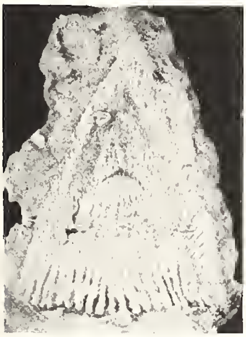
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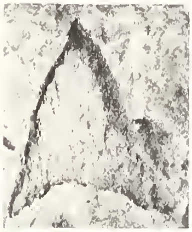
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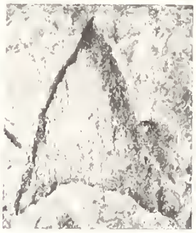

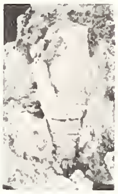
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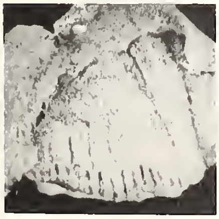
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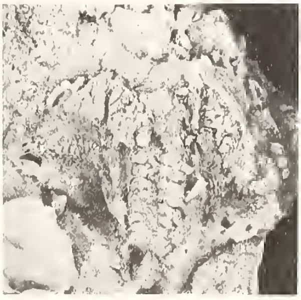
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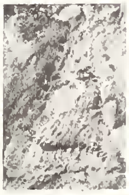
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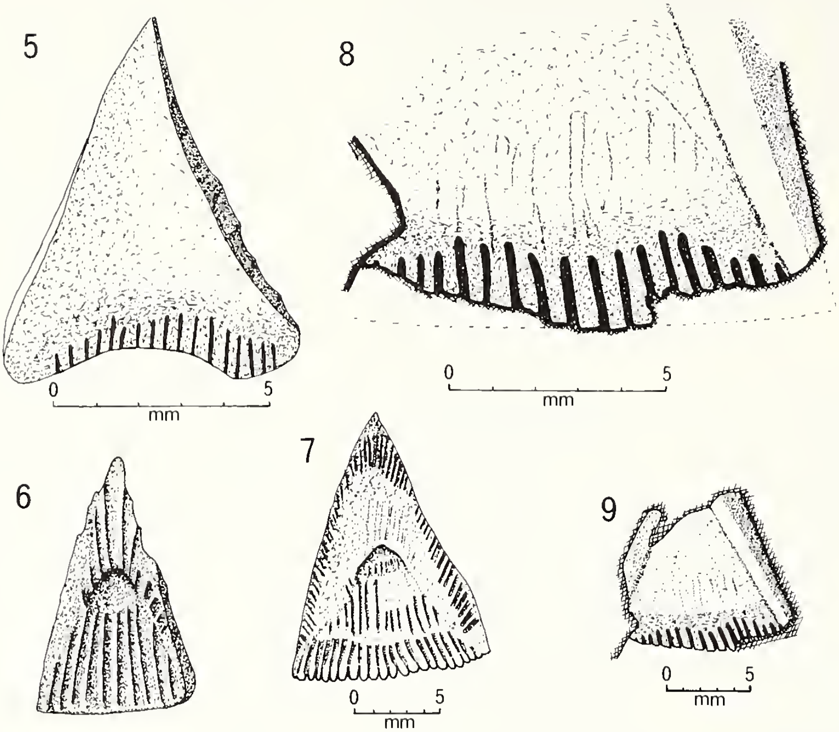
PAUL and COPE, *Blastoidocrinus*



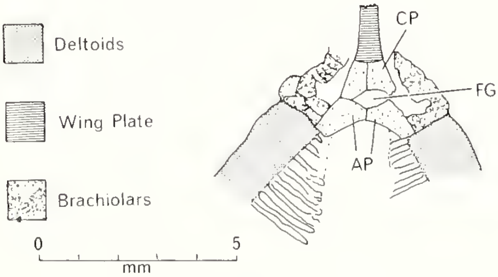
TEXT-FIGS. 5–9. Camera lucida drawings of isolated deltoids of *Blastoidocrinus antecedens* sp. nov. L. Arenig, Llangynog, South Wales. 5, paratype, external, NMW 78. 8G. 10 showing aboral cataspire slits, smooth surface, and weakly scalloped margins. 6, paratype, internal, NMW 78. 8G. 7, to show traces of cataspire canals. 7, internal surface of paratype NMW 78. 8G. 5 a large radial with many cataspire canals. 8, 9, external of same paratype (NMW 78. 8G. 5) to show thickened adambulacral margin, aboral cataspire slits, and weak traces of ornament. Larger scales refer to figs. 5–6, 8; smaller to figs. 7, 9.

This paratype is crushed and retains no traces of basal plates, but one of the preserved radials is strongly folded so that it may be inferred that the theca had a deep aboral depression into which the stem inserted, as in *B. carchariaedens*, the only other species in which the complete theca is known. In *B. carchariaedens* the basals are very small and lie entirely within this basal depression. This was probably the case in *B. antecedens* too.

Isolated deltoids reveal an almost smooth external surface with short cataspire slits aborally (text-fig. 5) and occasionally very faint grooves parallel to the slits and a little above them (Pl. 51, fig. 11; text-figs. 8–9). The cataspire slits are short and narrow, perhaps reaching 2·0 mm long by 0·2 mm wide in the largest plates. The lateral edges of the deltoids are thickened and often scalloped to a greater or lesser degree where the ambulacral flooring plates fit against them. This scalloping is much less obvious than that on isolated deltoids of other species of *Blastoidocrinus* (see, for example, Sprinkle 1973, pls. 34, 36, 37). Internally, the deltoids preserve traces of the catapire canals (text-figs. 6, 7) except in a small central area. In the adoral and lateral two-thirds of the deltoids cataspire canals converge, but in the aboral third they diverge slightly (text-fig. 6). Each canal must be bent, but it is virtually impossible to trace any one canal across these bends in the available plates.

Subvective system: there are five equal, parallel-sided ambulacra. In the holotype each bears two series of flooring plates, an outer series of rectangular plates, ten or eleven of which occur in each ambulacrum, and an inner series of smaller, pentagonal plates which meet at a zigzag suture and seem to bear a one to one ratio to the outer flooring plates. Thus it would seem that the number of outer flooring plates per ambulacrum (and probably the number of brachioles) approximately equalled the number of cataspire folds per deltoid. This suggests that there was an opening for the cataspire folds at the base of each brachiole beside the outer flooring plate, as in *B. carchariaedens*. The numbers of flooring plates and cataspire folds need not correspond exactly, since each deltoid receives cataspire canals from half of each adjacent ambulacrum. One external mould (Paratype NWM 78. 8G. 2; text-fig. 2) apparently shows two sets of flooring plates, while another (NWM 78. 8G. 3; Pl. 51, fig. 5; text-fig. 4) shows the ambulacral 'wing', a blade-like structure lying above the ambulacral food groove and against which the brachioles folded in life. In the holotype the ambulacra are about 8 mm long and 3 mm wide proximally; in one of the paratypes one ambulacrum reaches 11 by 4 mm. Externally the outer flooring plates are narrow and the inner ones make up most of the width of the ambulacrum; internally the reverse is the case. The external mould that shows the flooring plates best (text-fig. 2) apparently preserves no trace of 'wing plates', but another example does preserve the 'wing' (Pl. 51, fig. 5; text-fig. 4). This ambulacral structure differs a little from that described by Hudson (1907, pp. 111 *et seq.*; fig. 2, p. 105). Hudson's section shows outer flooring plates (which he called adambulacrals) forming the entire width of the ambulacrum internally and external to them a pair of what are effectively cover plates which bear the 'wing plates' above (i.e. externally). Food from the brachioles must have passed over Hudson's adambulacrals to a central food groove beneath the cover plates and the wing plate (see text-fig. 10). In *B. antecedens* it is difficult to make out the exact structure of the ambulacra, but clearly from the holotype (which is an internal mould), two series of plates *floored* the ambulacrum, not just the one shown in Hudson's section of *B. carchariaedens*.

Adorally, traces of a few brachioles are preserved on two paratypes. They are clearly biserial and very narrow. None is complete.



TEXT-FIG. 10. Cross-section through one ambulacrum of *Blastoidocrinus carchariaedens* Billings, type species of *Blastoidocrinus* (after Hudson, 1907, fig. 2, p. 105). AP, ambulacral plate; CP, cover plate; FG, food groove.

Discussion. This discovery extends the known stratigraphic and geographical ranges of the class Parablastoidea. *Blastocystis rossica* Jaekel comes from the Kunda Formation (Upper Arenig–Lower Llanvirn) of Pulkowa, Ingermanland, U.S.S.R., and was hitherto the oldest known parablastoid. All other parablastoids were known from North America; *Blastoidocrinus rossi* Sprinkle, *B. nevadensis* Sprinkle, and *B.? elongatus* Sprinkle from the Llanvirn; *B. carchariaedens* Billings from the basal Llandeilo, while both species of *Meristoschisma* come from the Llandeilo–Caradoc boundary in the southern Appalachians. The new species comes from close to the base of the local Arenig section at Llangynog and is the oldest known form.

FUNCTIONING OF THE CATASPIRES

Hudson (1915) in a stimulating paper concluded that the respiratory structures of true blastoids and the parablastoids differed from all other types of internal (i.e. endothecal) respiratory structures in echinoderms because the currents of sea water that flowed through them were generated (partly or wholly) by the brachioles of the ambulacra. He believed that food was carried along the brachioles by cilia which induced water currents as well. Naturally, he assumed that the current in the respiratory structures entered at the ambulacral pores and exited at the other end of the canals. Thus he regarded the two types of pore-structures in true blastoids and parablastoids as being fundamentally opposed in their current directions. In blastoids the currents entered the ambulacral pores and travelled towards the mouth to exit through the spiracles (at least in spiraculates), while in parablastoids the currents travelled away from the mouth to exit through the deltoid slits. Hudson (1915) designated these structures anaspires and cataspires, respectively. Examination of isolated deltoids of *Meristoschisma hudsoni* Sprinkle from the Benbolt Formation of Tennessee gives cause to believe that the currents in cataspires also travelled towards the mouth, i.e. *from* the deltoid slits to the adambulacral pores, as Sprinkle (1973, p. 165) has already suggested.

The reasoning is two-fold. First, externally the deltoid slits in *M. hudsoni* seem to be simple and very long and thin. Internally, each slit is obviously divided into a series of short slits and the cataspire canals are much wider. Now no animal can control the composition of the surrounding sea water. There is always a danger of canals becoming clogged with suspended particles. This danger can be avoided if the entrance to any canal is the narrowest point, because any particle capable of entering the canal can pass right through. Particles trapped at the entrance can pass along the slit or be removed by a brief reversal of the current. On the other hand, if the exit is the narrowest point, particles of a critical diameter might pass through the canal but become lodged at the exit. To clear them would require reversing the currents to carry the particle all the way back along the canal. This is inefficient at best, always assuming such reversal of currents is possible. Thus the morphology of the cataspire slits in the deltoids of *M. hudsoni* suggests that they were entrances not exits.

The second point is that with any system of endothecal canals there is always a danger of recycling. Deoxygenated sea water might leave one canal and then enter another or be sucked back into the same one. Again this is inefficient. Recycling can be minimized by locating exits together and away from entrances, but also by inducing a strong excurrent which is carried away from the thecal surface to mix with normal sea water before there is any chance of re-entry. Since current velocity is inversely proportional to the cross-sectional area of the canals, constricting the exit boosts the excurrent. Note that the exit may have a smaller cross-sectional area but still be wider, than the entrance. The ideal canal would have a slit-like entrance and a circular exit, the total area of which was less than that of the entrance. Once again then, the narrow deltoid slit of *M. hudsoni* has the form of an entrance, while the more or less circular adambulacral pores have the morphology of exits.

The conclusion that cataspire currents flowed from the deltoid slits towards the adambulacral pores seems inescapable. The term 'cataspires' may be retained despite its misconceived origin, especially as the alternative term 'anaspires' has never been used since Hudson coined it. Furthermore, Hudson's supposition that the brachioles produced water currents is probably wrong. They merely transport boluses of mucus and food, so the exiting currents from the cataspires need not have worked against supposed feeding currents.

As Sprinkle (1973, p. 164) has pointed out, aborally the internal cataspire canals of *Meristoschisma* are just attached to the adoral edge of the radials, while their adoral ends are shared by a pair of ambulacral plates which surround the adambulacral pore. Nevertheless, the main bulk of the canals in all parablastoids is attached to, and lies under, a deltoid plate and could only increase in length at the two margins of the deltoid. However, Hudson (1907, p. 106) noticed that cataspire canals were deepest in the central portions of the deltoids. The peculiar and unique arrangement whereby the bulk of these canals lies under the deltoids inevitably involves a more complex pattern of growth than in the respiratory structures of rhombiferans or blastoids. Existing cataspire canals could only increase in depth by resorption within the canal and resecretion outside it (i.e. within the thecal cavity). In blastoid hydrospires and in all cystoid rhombs the canals cross a plate suture and are more or less equally developed in two plates. As the plates grew, existing canals could be deepened at the suture. Thus once a portion of a canal was formed, there was no need to alter it in any way subsequently. The relatively complex and inefficient growth pattern in parablastoids may partly account for their lack of success.

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A NEW SPECIES OF THE LUNGFISH *DIPNORHYNCHUS* FROM NEW SOUTH WALES

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Abstract. A new broad-headed species of the primitive lungfish *Dipnorhynchus*, *D. kiandrensis*, is described from an isolated skull roof found in the Emsian (Lower Devonian) Lick Hole Limestone at the Ravine, near Kiandra, New South Wales. It is slightly older than the specimens of *D. sussmilchi* previously described. The existence of extra bones, particularly T and 14, in the cheek of this genus is substantiated. Arguments favouring the existence of H between Z and A in primitive dipnoans are presented. The ethmoidal canals are shown to be less complex in *Dipnorhynchus* than in *Chirodipterus*. Fine tubules apparently belonging to the same general system as the ethmoidal canals are found between the dermal roofing bones and the neurocranium over a wide area of the skull.

A skull roof of *Dipnorhynchus* from the Lick Hole Limestone in the Ravine, near Kiandra, New South Wales, provides new information on the roofing bone pattern of primitive lungfishes. The specimen was recovered from locality C54 of Flood (1969), which lies well within the range of the conodont *Polygnathus dehiscens* Philip and Jackson. Further north at Taemas and Wee Jasper this species is not known to occur in rocks younger than the Cavan Bluff Limestone (text-fig. 1). Abundant brachiopods occur at the locality, especially *Spinella yassensis ravinia*, *Athyris waratahensis*, *Howittia multiplicata*, and *Uncinulus australis*. In addition to the brachiopods, the limestones contain a variety of molluscs and rugose corals.

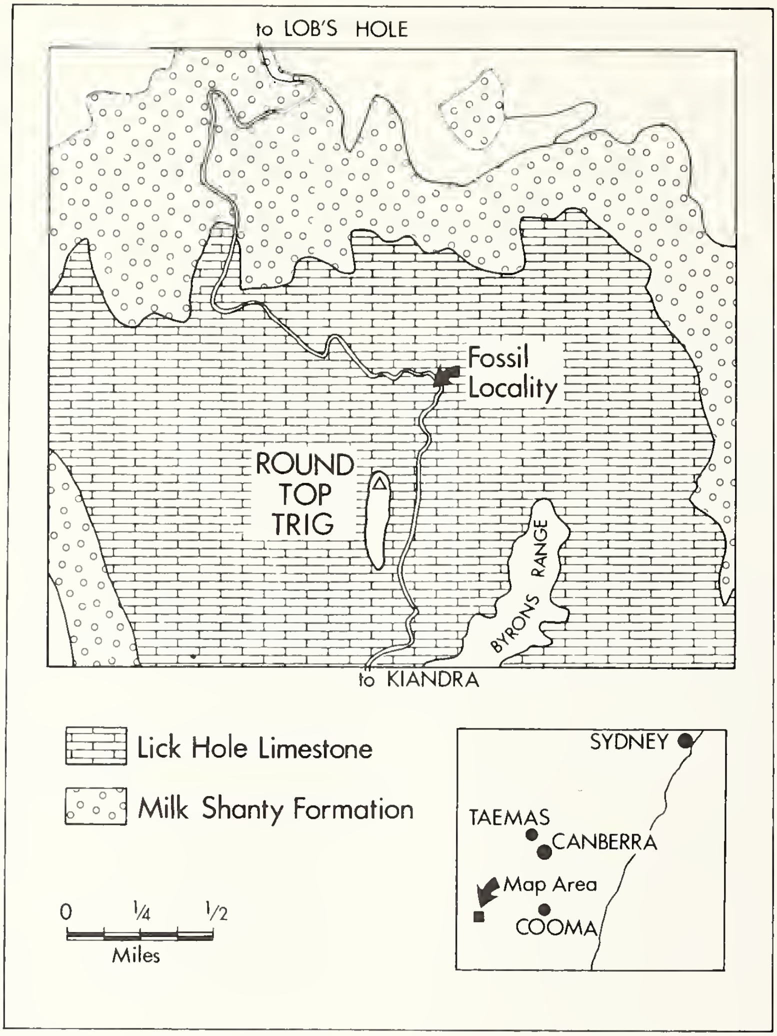
The Lick Hole Limestone is up to four times as thick as the Cavan Bluff, and it has a greater faunal diversity, including some genera, such as the rugose coral *Chalcidophyllum*, found only in rocks above the Cavan Bluff at Taemas and Wee Jasper. It may record a period of time represented by the Cavan Bluff Limestone and at least part of the Majurgong Shale at these localities. A slightly different view is presented by Strusz *et al.* (1972, fig. 2).

Prior to this discovery, the oldest skull roofs of *Dipnorhynchus* were from the *Spinella yassensis* Limestone which, on the basis of either of the above correlations, is a little younger than the Lick Hole Limestone. The new specimen, therefore, is the oldest known representative of the genus in Australia.

Rocks at the locality consist of well-bedded dark-grey limestone interstratified with dark calcareous mudstones. There is no doubt that the environment was marine and the facies is closely comparable with that from which the genus has been obtained previously. No other bone has been found at the locality or along strike from it.

The specimen was found in two isolated pieces of rock on the same outcrop. The pieces fitted together well, but not perfectly, and as a result the reconstruction may be slightly foreshortened along the join. Some of the bones had been removed by weathering, leaving an impression of the bone pattern on the surrounding matrix. By filling the vacated spaces with resin it has been possible to restore these parts of the skull. The right posterior corner of the roof is well preserved so that the outline of Y_2 can be clearly determined, but the median posterior edge is badly eroded, much of I having been removed, leaving no indication of the outline of A. Apart from this, by piecing together information from left or right, or both, it has been possible to reconstruct the roof with the exception of the D bones and those immediately in front of them (see Pl. 52, figs. 1, 2; text-fig. 2).

[Palaeontology, Vol. 25, Part 3, 1982, pp. 509-527, pls. 52-53.]



TEXT-FIG. 1. Locality map, the Ravine, near Kiandra, New South Wales.

EXPLANATION OF PLATE 52

All specimens *D. kiandrensis* sp. nov. (35642 ANU)

Figs. 1–2. Dorsal and ventral views of skull roof.

Fig. 3. Anterior view of snout to show canals of the ethmoid capsule and the anterior part of the lateral-line canals and the ethmoid commissure (arrowed).

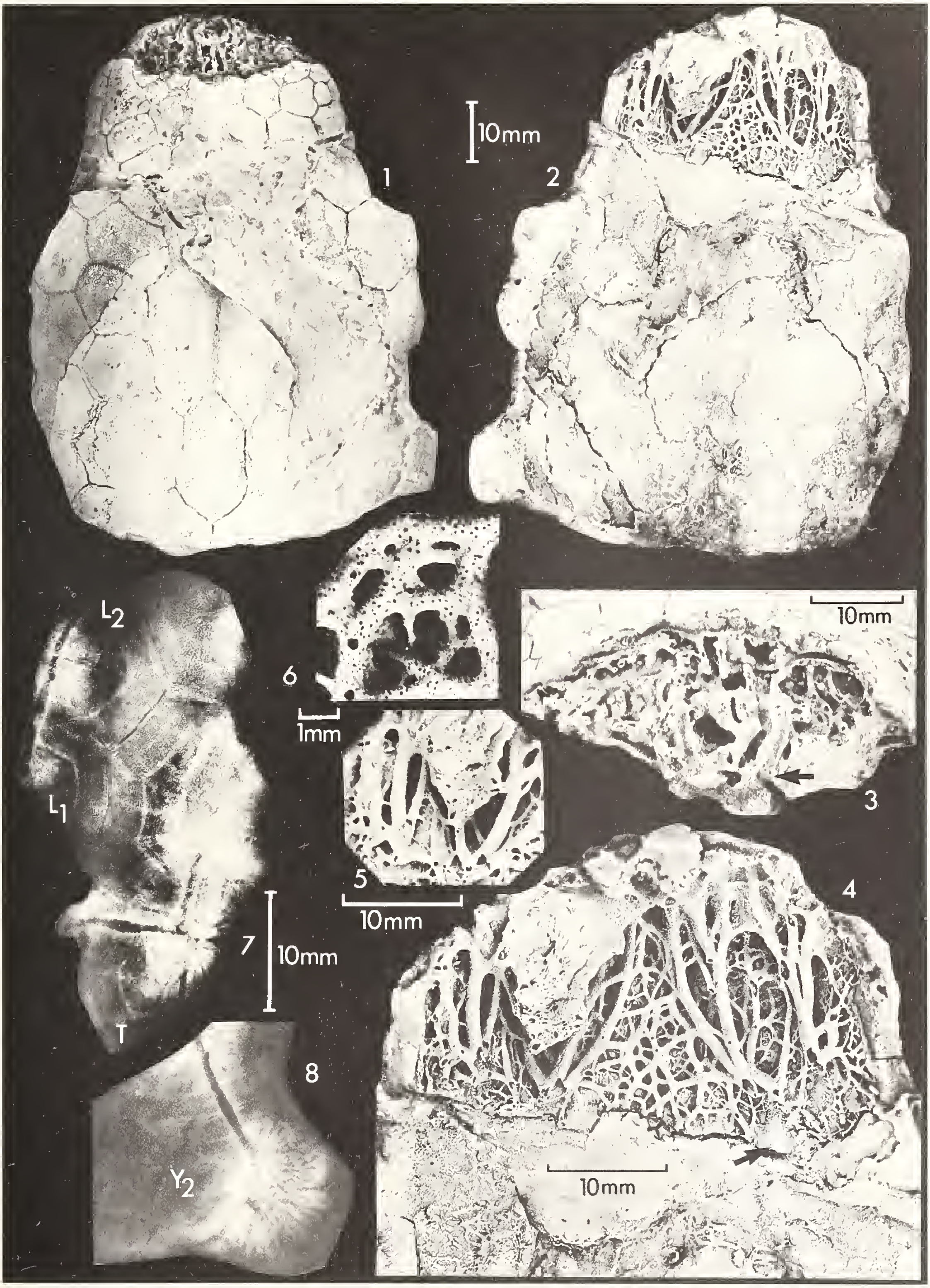
Fig. 4. Enlargement of ventral view of ethmoid capsule. Note the fragment of the roof of the nasal capsule on the left.

Fig. 5. Part of ethmoid capsule with specimen tilted to the left to show the orientation of the canals entering the ethmoid capsule from the nasal capsule.

Fig. 6. Detail from fig. 4 to show structure of the canal bones.

Fig. 7. X-radiographs from right side of skull showing the linkage of the lateral-line canals in bone T and the main canal passing through L_1 and L_2.

Fig. 8. X-radiograph showing the lateral-line canal in Y_2 and part of Y_1 with numerous tubules.



CAMPBELL and BARWICK, Devonian lungfish

SYSTEMATIC PALAEONTOLOGY

Infraclass DIPNOI Müller, 1844
Family DIPNORHYNCHIDAE Berg, 1940
Genus DIPNORHYNCHUS Jaekel, 1927
Dipnorhynchus kiandrensis sp. nov.

Etymology. From the village of Kiandra, the nearest settlement to the type locality.

Holotype. 35642 ANU, Geology Department, Australian National University, Canberra.

Horizon and locality. Lick Hole Limestone (Emsian), the Ravine, near Kiandra, New South Wales, Australia.

Differential diagnosis. Skull transverse; most roofing bones more transverse in outline than their homologues in *D. sussmilchi*; interorbital width *c.* 183% of the length of the bones B+C; only two or three lateral line bones between M and the sharp medial flexure of the canal on the snout; bone 14 extending up into the Y_1–Y_2 line; cheek below the Y_2–14–T line probably mobile; operculum lying below the level of the lateral edge of Y_2.

Discussion. This is only the third good skull roof of *Dipnorhynchus* to be found, and consequently little can be said about species variation within the genus. The two skulls of *D. sussmilchi* show considerable differences in the expression of the C bones, the relative sizes of Y_2 and Y_1 and apparently in the number of preorbital bones, and it is difficult to know if this new roof just extends the range of variation in what must be a variable species, or if it is a separate species. Early dipnoans such as *Dipterus valenciennesi* show a wide range of variation patterns in the skull roofs, and species of *Dipnorhynchus* may be expected to show similar ranges.

However, the skull specimens of *D. sussmilchi* come from the *Spinella yassensis* Limestone which is appreciably younger than the Lick Hole Limestone, and the early part of the Devonian is known to be a period of rapid dipnoan evolution. This age difference and the points listed in the diagnosis which show that the new roof can be distinguished morphologically from the two specimens of *D. sussmilchi*, have inclined us to the definition of a new species.

SKULL ROOF

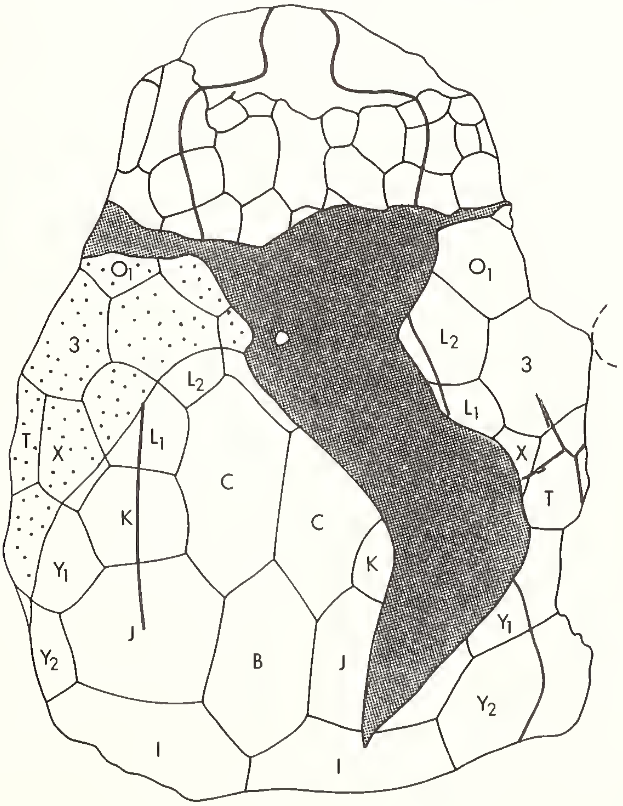
Nomenclature of roof and cheek bones. Dipnorhynchus is the oldest dipnoan in which the roof and some of the cheek are known. *Uranolophus*, which is probably a little older, lacks the lateral parts of the roof and cheek. The standard nomenclature for the bones of the dipnoan skull roof and cheek was developed for *Dipterus*. Attempts to apply this nomenclature to *Dipnorhynchus* by Westoll (1949), Lehmann and Westoll (1952), White (1965), and Denison (1968) *inter alia* led to widely differing interpretations. Thomson and Campbell (1971) therefore attempted to list the criteria by which the bones in these primitive forms could be recognized, and showed that the interpretation offered by Denison was the most satisfactory, though he did not include all the bones known at that time. They also showed that there were bones present on the post-orbital part of the skull of *Dipnorhynchus* that were unknown in *Dipterus*, and they inferred the presence of others. These previously unrecognized bones were named and criteria for their identification were listed.

Having done this for the most primitive genera, they proceeded to use what is known of the broad pattern of evolution of the dipnoans, in conjunction with stated criteria for the recognition of fusion or elimination of bones, in an attempt to identify the bones of the roofs of later Palaeozoic genera. In doing this, they were cognizant of the difficulty of using the positions of bones relative to one another as a basis for the identification of bones on the anterior part of the skull, particularly those in the L–N and O–P series. On the other hand, emphasis was placed on the value of canal-canal and canal-pit line junctions in identifying certain bones, particularly X, K, T, and 5; on relations to the neurocranium in identifying others, particularly I, which meets the dorsolateral crista, and D, which is associated with the pineal openings; and on the relation to the palatoquadrate, particularly Y_1 and Y_2.

Since then two important papers on bone nomenclature in the dipnoans have been published by Miles (1977) and Graham-Smith (1978). Miles, basing his conclusions on the theoretical work of Jardine (1969), has strongly criticized the work of Thomson and Campbell (1971), and *inter alia* claimed that the T of *Dipnorhynchus* is a misidentified 4 and that H does not exist. Graham-Smith was also doubtful of the validity of the arguments used for the existence of H. It is not our intention to offer a general discussion of the theoretical issues involved. This we intend to do as part of a later paper on dipnoan evolution. This newly discovered specimen, however, permits us to check previous conclusions on bones T and H, as well as the bones of the posterior part of the cheek. In carrying out these checks we will attempt to show that in discussing the homologues of structures forming complex patterns, it is essential to argue from the most complicated to less complicated situations; that parsimony is a useful guide only in deciding between equally probable hypotheses; that lateral line canals in certain parts of the skulls of primitive forms lie in tubes made of a bony mesh below the dermal bone proper; but that lateral line canal-bone relationships provide the best guides available for the identification of bones on some areas of skull roofs, though they must be used in conjunction with other data.

Roof bones of D. kiandrensis. The roofing bones show a pattern very similar to that of *D. sussmilchi*, the differences being largely ones of proportion (text-fig. 2).

Bone Y_2 is complete on the right side. Its posterior edge is concave in outline, and the bone has a finished margin over most of its width. The shape of the postero-lateral corner shows that the operculum lay entirely below the level of the lateral edge of the bone, unlike the situation in later species in which the operculum truncates the posterolateral corner. This means that the operculum was unusually low in relation to the skull roof.



TEXT-FIG. 2. Diagram of dorsal view of skull roof of *Dipnorhynchus kiandrensis* sp. nov. (35642 ANU). The dark stipple indicates the area of plastic reconstruction and the light stipple the area of impression on the surrounding matrix. × 1·2 approx.

The outline of Y_1 is known from the left side of the specimen, and part of it is preserved on the right. It is a large bone also.

Bone I is incomplete on both sides, but on the right sufficient of it is preserved to permit its outline to be approximately reconstructed from X-radiographs. These show it to be a very transverse bone—proportionately even more so than in *D. sussmilchi.* Although it cannot be proved beyond doubt, the median suture between the I bones is probably proportionately longer than in *D. sussmilchi.*

Bones J, K, L_1, and L_2 are similar to those of *D. sussmilchi* in all respects except their more transverse outlines. Bone X is more equidimensional than it is in *D. sussmilchi.* The result of these different proportions is that the interorbital distance measured between the upper edges of the orbits around the dorsal curvature is 183% the length of bones B+C, whereas in *D. sussmilchi* the corresponding figure is 155%.

Bones B and C are as in the second specimen of *D. sussmilchi,* 18815 ANU—i.e. B is pointed front and back, and the C's are clearly separated. The maximum width of the skull measured around the curvature between the lateral extremities of the Y_2 bones is 219% the length of B+C, whereas in *D. sussmilchi* the corresponding figure is 206%.

The bones D have not been preserved, but the sediment infill of the pineal foramen has been retained on the internal mould. This lies between the anteromedial corners of the L bones as in *D. sussmilchi.* The pineal cavity in the visceral surface of the skull is broad, and a distinct tube occupies part of the right side, without expansion of the termination. There is no evidence of a duct on the left side.

Bone 3 is complete on the right side and shows the characteristic bevelled edge of an orbital marginal bone. Its overall shape is very similar to that of bone 3 in the holotype of *D. sussmilchi* except that it is relatively wider. In front of it, 0_1 is preserved on the right side and most of 0_2 is present on each side. 0_1, at least, is of the *sussmilchi* type.

Although part of the roof is missing along the line of junction of the fragments, and identification of most of the individual bones in the ethmoid region is impossible because of this and the natural complexity of the pattern, it is still possible to make some important observations. The transverse part of the lateral line canal on the snout passes through three bones on the left side, and probably only two on the right, whereas in *D. sussmilchi* (18815 ANU) there are four bones on each side. On any reassembly, the number of lateral line bones between M and the sharp medial bend on the snout can be no more than three, and probably only two; in *D. sussmilchi* there are at least three and on one specimen five. Bone 0_2 is small, and there are two or three small bones carrying the infraorbital lateral line anterolateral to 0_2. These must be 1_1, 1_2, and 1_3. This is similar to the situation in *D. sussmilchi.* In summary, the bones in the snout are definitely fewer in number than in the ANU specimen of *D. sussmilchi,* and probably slightly fewer than in the holotype of that species, though the bones in that specimen are partly obscured by cosmine.

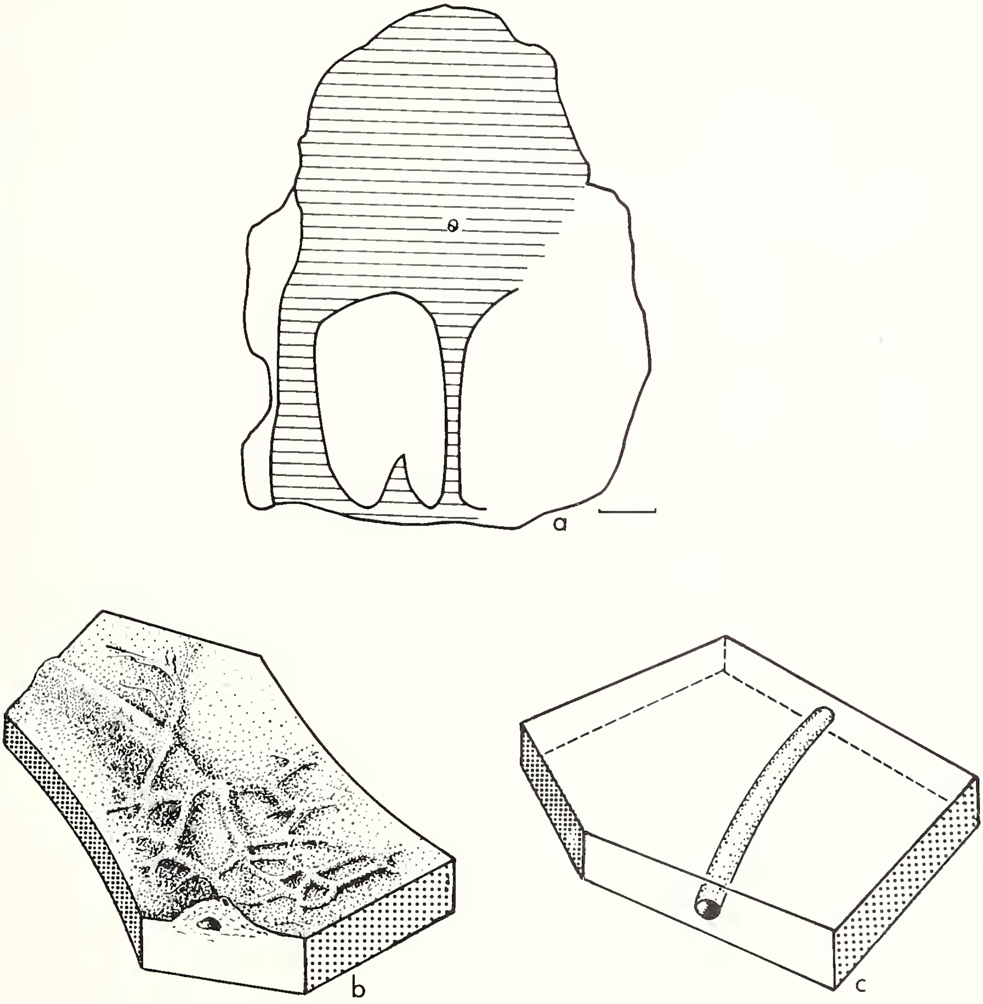
Most of the snout has been eroded, but a tiny part of the upper lip and the paired dermal thickenings on either side of the internasal septum are preserved, permitting a reasonable reconstruction of the snout profile to be made. It does not appear to have been significantly different from that of *D. sussmilchi.*

LATERAL LINE SYSTEM

General. The lateral line canals can be traced by pores, X-rays, and exposed traces on broken surfaces. Over the whole skull the canals are buried deeply in bone, but there are two quite distinct relationships between the canals and the dermal bones determined by the presence or absence of neurocranial bone beneath the dermal bone (text-fig. 3).

On all the specimens of dipnorhynchids and *Chirodipterus australis* we have examined, the form of this junction is similar, and is shown on text-fig. 3. On our new species, where the neurocranium and the roofing bones enclose a space the lateral line canals lie in thickened tubes formed of cancellous bony tissue along the visceral surface of the dermal bones. These thickened tubes are easily visible because they form ridges. They are covered by a continuous thin periosteal layer in the same way as the remainder of the bone surface. Examples are shown on Pl. 52, fig. 4 and Pl. 53, fig. 7, where they are indicated by arrows. Where no neurocranial bone underlies the dermal bone, the canals are buried deeply in the bones, and usually no ridge is visible on the visceral surface of the bones. The same pattern occurs on *D. sussmilchi* and on a specimen of an undescribed dipnorhynchid genus from Cave Island, near Wee Jasper, New South Wales.

The two relationships are thought to be of importance with regard to the possible movement of a canal relative to the ossification centres of the dermal bones during growth. If a canal is buried in a bone, it must pass close to the centre of ossification unless resorption takes place along one wall of the canal and deposition on the other, thus allowing it to move away from the centre during ontogeny. This should show on X-radiographs because the radial bone structure would be disrupted. It is significant that such disruption apparently occurs in bone T where the size and shape of the cross linkage of the canals implies modification during growth. However, X-radiographs show the canal passing through the undisturbed bone centres elsewhere. Furthermore, some resorption must take place to permit the canals to increase in diameter during growth. If the canal lay in a special thickening below the main dermal bone and partly under the influence of the osteoblasts of the neurocranium, it may be easier for the canal to move by resorption and redeposition, and without leaving any distinguishable effect on the radial bone structure. This also opens the possibility for a canal to pass from one bone to another during ontogeny, because peripheral bone growth would no longer be a limiting factor.



TEXT-FIG. 3. *a*, form of junction between dermal bones and neurocranial bone in *Dipnorhynchus kiandrensis* sp. nov. Ventral view of skull roof; crosshatched area indicates dermal/neurocranial bone junctions. *b*, lateral-line canal lying on the ventral surface of a dermal bone. *c*, lateral-line canal penetrating a dermal bone. (Scale = 10 mm.)

In the early stages of dipnoan evolution, the lateral line canals were buried in or below the dermal bone, but by the Late Devonian the canals were usually buried deeply in the bone even though the bones are cosmine covered. In *Chiropdipterus* this is usually the situation, though the canal is exposed on the inner surface as it passes under the neurocranial cover (see Pl. 53, fig. 11) in an occasional specimen. With the loss of the cosmine layer in Carboniferous and later forms, the canals came to lie on the bone surface and then in the skin covering the bones, and so other possibilities of canal movement relative to ossification centres become available.

Lateral Lines of D. kiandrensis. The main lateral line, which lies in a thick tube below Y_2, makes a subangular change in direction near the centre of ossification of that bone. A similar change is noted in *D. sussmilchi*, though it was not shown by Thomson and Campbell. Numerous tubules, many of which bifurcate, spread towards the lateral edge of this bone. In Y_1 the number of tubules is less.

The bone tissue of X, as opposed to its outline, is preserved as a fragment on the right side of the specimen, and the canal can be seen to make a right-angled bend at its centre before passing to T. Canals pass from T to 3, 4, and 14 (see below). These canals do not meet at a point, but rather have a linkage in T as shown on Pl. 52, fig. 7. There are numerous tubules on the lateral half of this bone also.

There is nothing unusual about the supraorbital canal in J, K, L_1, and L_2, but it is better shown on the rostral region than in the specimens of *D. sussmilchi.* The paired canals approach each other closely a short distance above the lip, and join with a short thick commissure. The pore terminating the canal lies in the inner edge of the external naris. As the canal passes over the nasal capsule, the usual thick spongy tube is formed around it.

A fragment of the infraorbital canal is preserved on the right side, passing under the 1 bones where it also is encased in spongy bone. It seems to terminate abruptly well up on the snout, though the surface is not well enough preserved to show the nature of the terminal pore.

The occipital commissure is not preserved, but its inferred character will be discussed below.

The only pit lines on the skull are on I, and they are partially preserved on the left side. There is a long transverse line and apparently a shorter posterolaterally oriented line of the same type as those on *D. sussmilchi.*

BONES OF THE CHEEK

On each side there is a bone behind 3 and lateral to X, the one on the left being incomplete and preserved as a cast, but the one on the right being complete. This is the bone T of Thomson and Campbell (1971). X-rays show that it receives a single canal from X, but three canals issue from it—one to bone 3, a second anteroventrally, and a third posteroventrally. The X-rays also show clearly that the canals do not meet at a point, but rather approach one another, the junction being effected by a cross canal. This bone is clearly not a circumorbital.

EXPLANATION OF PLATE 53

Figs. 1, 2, and 3. Lateral and dorsal views of an almost complete skull of *Chirodipterus australis* (35638 ANU).

Fig. 4. Lateral view of one of the largest specimens of *C. australis* (35636 ANU).

Fig. 5. Skull of an almost complete specimen of *C. australis* (35640 ANU). Note the presence of bones Z and H in the extrascapular series.

Fig. 6. Ventral view of portion of skull roof medial to bones 3 and T in *D. kiandrensis* sp. nov. showing the tubules between the dermals and the neurocranium. Arrows indicate foramina where the tubules emerge through the neurocranial wall.

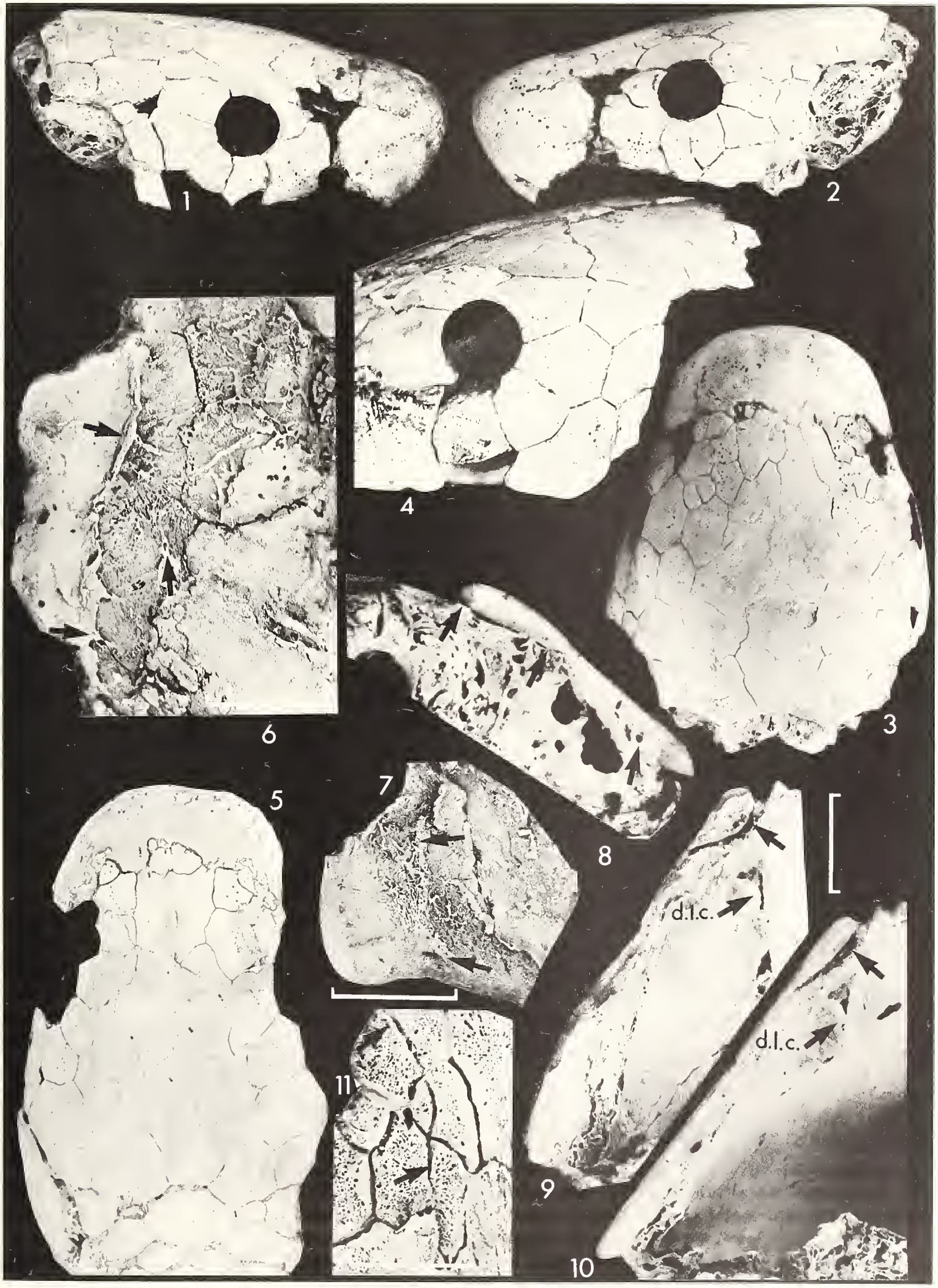
Fig. 7. Ventral view of bone Y_2 of *D. kiandrensis* sp. nov. showing the lateral-line canal lying in a thickened tube overlaid by fine tubules.

Fig. 8. Posteromedial view of the rear of the skull of *Chirodipterus australis* (35639 ANU) showing the open lateral-line canal passing under I and the buried canal Y_2 (both arrowed).

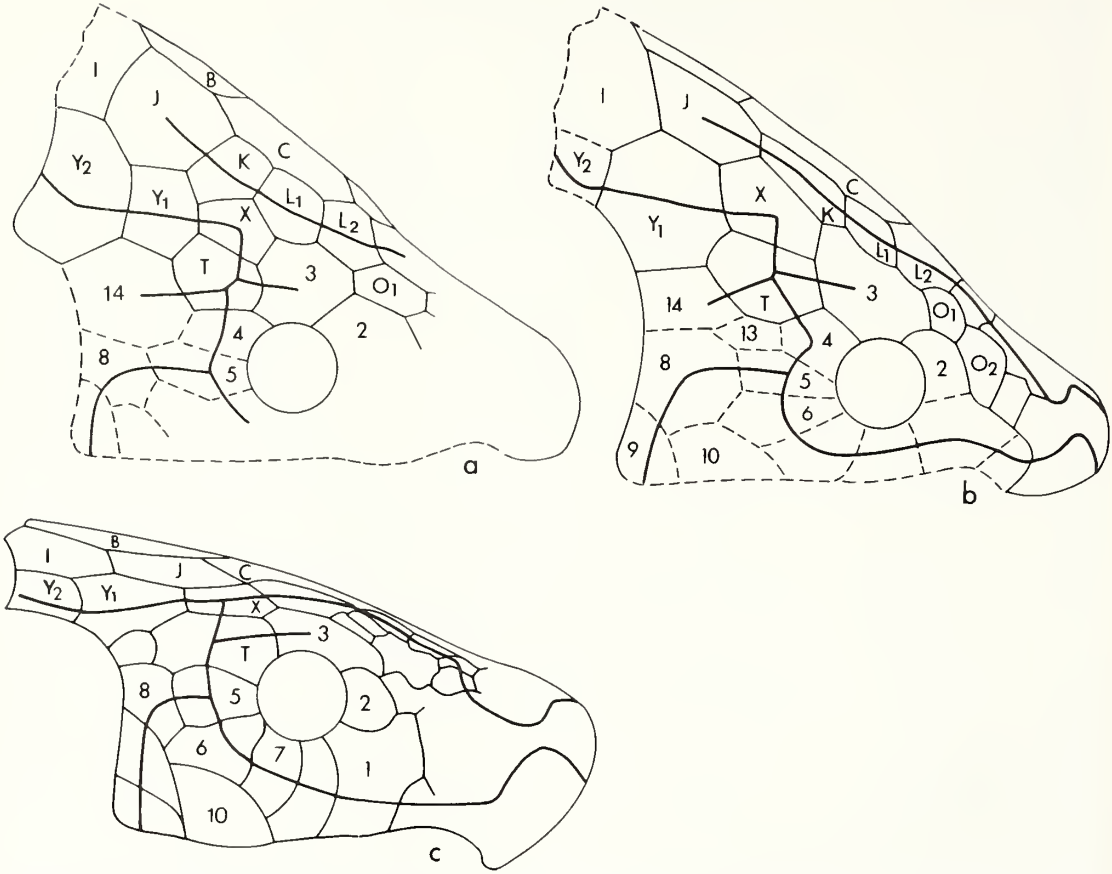
Figs. 9 and 10. Posteromedial and posterior views of the rear edge of the skull of *Dipnorhynchus sussmilchi* (18815 ANU) showing the occipital commissure of the lateral-line canal in I and the tube for the lateral-line canal under Y (both arrowed). d.l.c., dorsolateral crista.

Fig. 11. Ventral view of roofing bones of *Chirodipterus australis* (same specimen as in fig. 4), showing the lateral-line canal emerging from within the bone to lie in an open channel lateral to bone C (arrowed).

The scale bars are all 10 mm long. Figures without scale bars are natural size.



CAMPBELL and BARWICK, Devonian lungfish

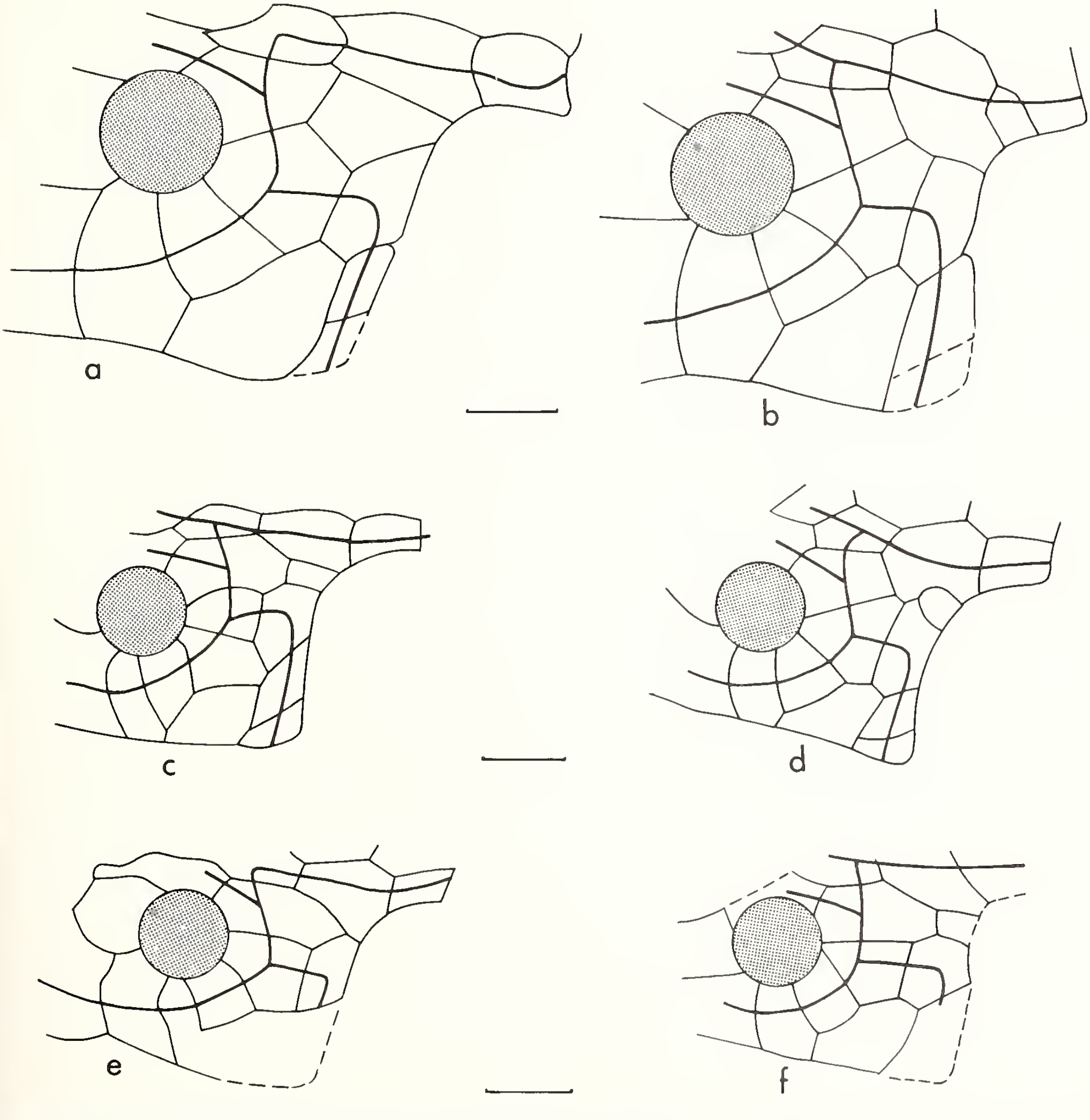


TEXT-FIG. 4. Lateral views of the right sides of the skulls of *a*, *Dipnorhynchus kiandrensis* sp. nov. *b*, *Dipnorhynchus sussmilchi* based on the holotype. *c*, *Chirodipterus australis* based on 35638 ANU. In *a* the lower part of the cheek involves the minimum number of bones possible. In *b*, which is modified from Thomson and Campbell, 1971, fig. 7A, an alternative reconstruction omitting bone 13 and increasing the size of bone 4 is possible.

The anteroventral canal from it must pass into a circumorbital in the *position* of a normal bone 4, and the posteroventral canal must pass into what would have been a large bone (14 of Thomson and Campbell), fitting into a deep embayment between Y_1, Y_2, and T (text-fig. 4*a*). It is clear from the shape of the bone Y_2 that the operculum must have occupied the space beneath it, and that there is no room for a bone 15. The large size of bone 14 is confirmed by the orientation of the lateral line canal passing into it from bone T, leaving little space for a bone 13. Thus, irrespective of the homologies decided upon, it is clear that there were at least three bones (viz. 4, T, and 14) of moderate to large size in *Dipnorhynchus* between the orbit and the operculum filling the space occupied by 4 in *Dipterus*. The pattern and number of these bones varies but, in so far as the evidence goes, bone 14 is higher on the skull and tends to break the Y_2-Y_1 line more in *D. kiandrensis*. This specimen also suggests that the bones of the cheek below the Y_2-14-T line were not fused but capable of movement, the lateral edges of Y_2 and T being clearly bevelled, whereas in the type of *D. sussmilchi* there seem to have been normal sutures in this region.

Discussion. Having established that there are more bones than Miles was prepared to admit, the question of their homologies must now be broached. In particular, it is necessary to examine the claim (Miles 1977, pp. 230, 249) that T is really 4 that has been misidentified. In order to conduct a discussion, it is proposed to use the terminology suggested by Thomson and Campbell for 4, T, and 14, simply so that enough symbols are available. Of course, the symbol 4 must be used for the homologue of 4 in *Dipterus* where it was defined, and it may be that the above usage will prove to be incorrect.

Any interpretation must take account of the disappearance of bone 14, and with it the posteriorly directed canal it contained, for such a canal is not found on any later lungfish. No specimen of *Dipterus* known to us has a bone in the position of 14 (i.e.) below Y, above 8, and bordering the operculum. However, in the ANU Gogo collection of *C. australis* five specimens have nine cheeks sufficiently well preserved to determine the presence or absence of a bone between 4 and the operculum. Of these nine cheeks, three have no extra bones in this position, five have one bone, and one specimen possibly has two (Pl. 53, figs. 1, 2, 4; text-fig. 5). These bones never contain a



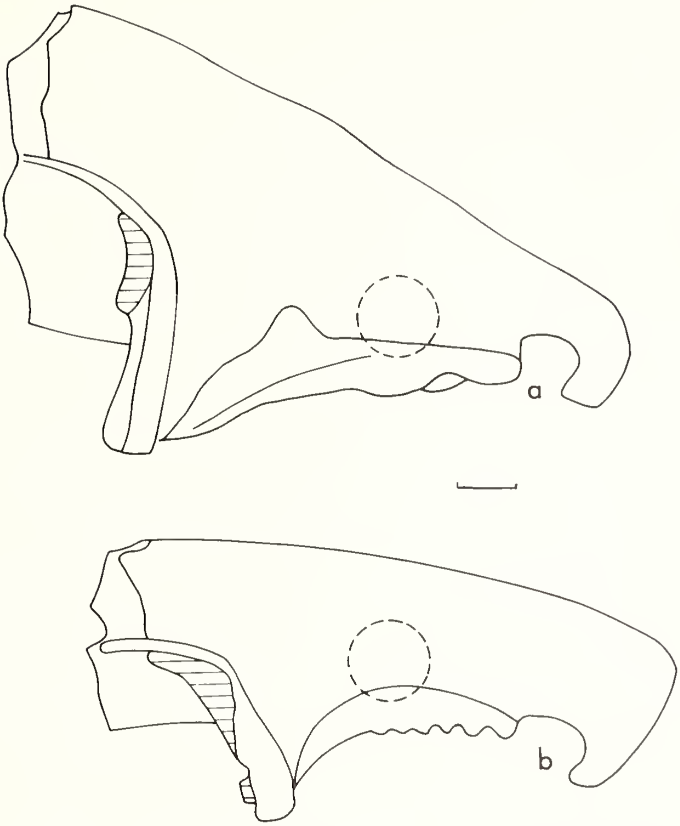
TEXT-FIG. 5. The cheeks of 4 specimens of *Chirodipterus australis* to show variation. *a* and *b*, the cheeks of 35636 ANU, in the same orientation; *c* and *d*, 35638 ANU; *e*, 21639 ANU; *f*, 35637 ANU. (Scale = 10 mm.)

lateral line canal. Because of their sporadic occurrence and the absence of a canal, it may be best to regard bones in these positions as anamestic, rather than 14's (or 15's). This information is intended to demonstrate that in at least one Late Devonian genus with a cheek relatively longer than that of *Dipterus*, there are extra bones forming a pattern like that postulated for *Dipnorhynchus*, and that the cheek figured by Miles (1977, fig. 117) for *C. australis* is atypical in having only bone 4 between the orbit and the operculum. What then has happened to 14 in those genera in which 4 runs the whole length of the cheek? The two possibilities are that it has fused with T or that it has become progressively smaller and has been eliminated.

It is known that bone 8 in *Dipnorhynchus* is large and equidimensional, but as the cheek became shorter in *Dipterus* and *Chirodipterus*, 8 also became shorter, whereas the posterior circumorbitals remained equidimensional or even elongate. Bone 8 cannot be eliminated because there must be a bone behind 5 to carry the lateral line to the lower jaw, though it may take up less space by moving to a posterolateral position on the cheek. The available evidence suggests that the shortening of the cheek was accomplished by the shortening of the posterior bones in the cheek, and therefore one might expect that bone 14 was shortened. Although it carried a lateral line, unlike bone 8 there was no functional reason for retaining it in a short cheek. In addition, it has not been appreciated previously that the height as well as the length of the cheek diminished considerably from *Dipnorhynchus* to *Chirodipterus* and *Dipterus* (text-figs. 4, 6). Although the cheek bones are not known in the first genus, the height of the whole cheek can be estimated from the position of the palate and the quadrates. Some of this height in *Dipnorhynchus* is accounted for by the size of Y_2 and Y_1, but much of it is taken up by T, 13, and 14. Consequently, during evolution there was a tendency for 14 to decrease in height as well as length, and as it was not functionally necessary as a canal carrier, a stage must have been reached where it did not develop, its residual space being occupied by the bone in front.

For the reconstructions of the cheek of *D. sussmilchi* given by Thomson and Campbell there are no bones 4 and 13 available as controls. They were reconstructed to fit the shapes of the spaces whose upper edges were determined by 3 and T (text-fig. 4*b*). In addition, the radiation centre of 4 can be approximately fixed from the orientation of the canal that enters it from T. A similar reconstruction is required by the present specimen. There is no concern about labelling 13, but is 4 correctly identified? Could it not equally well be 5, as it would presumably have to be if the unsupported statement of Miles (1977, p. 230) that T is really 4 is to be accepted? The shape of the loose 8 seen in a specimen from Buchan can be interpreted to mean that this would be impossible, but that interpretation certainly cannot be conclusive. Could the situation be like that in the only known cheek of *Holodipterus gogoensis* (Miles 1977, pp. 238, 248) where 4 is shown as a very large bone withdrawn from the orbit, containing the canal running forward on to 3, and with a process on 3 running around the back of the orbit to meet 5? There are two problems with such a solution. In the first place, none of the three examples of bone 3 that we have from *Dipnorhynchus* show any sign of extending around the posterior margin of the orbit. In the second place, it cannot be assumed that the identification of 4 in *Holodipterus* is correct—that is only one possible solution, and it cannot be accepted by fiat. Would Miles have come to his solution if the more complex pattern of *Dipnorhynchus* had been known before that of *Dipterus*, and its bones used as the basis for the system of nomenclature? This highlights one of the main difficulties in not starting from the most complex known organization when attempting to determine relationships in a reducing bone system (Thomson and Campbell 1971, p. 20). It also shows how an apparently parsimonious approach can lead to the too facile adoption of what seems to be a simple solution to a problem when more complex ones should at least be considered. Parsimony is useful as a means of choosing between equally probable hypotheses, but in its application there is a not uncommon tendency to rule out the more complex solution without adequate consideration of the relative probabilities of two hypotheses. In fact, the concept of equal probability is very difficult to apply in real situations.

As we have seen, irrespective of how they are named, there were bones on the positions labelled 4, 13, and 14 by Thomson and Campbell in *D. sussmilchi*, and that as the cheek became shorter and lower, bone 14 and the canal to it were lost, together with bone 13. Bones T and 4 may have



TEXT-FIG. 6. Lateral view of skulls of *a*, *Dipnorhynchus sussmilchi* and *b*, *Chirodipterus australis* to show relationships of palate and the lateral wing of the neurocranium to the outline of the skull roof. Hatched area indicates the hyomandibular and hyosuspensory attachment areas. (Scale = 10 mm.)

adjusted in two different ways. In one group, T was retained and moved closer towards the orbit, while 4 was progressively reduced in size. If T did not reach the orbit the posterior part of 3 would expand and may ultimately meet 5. The canal from T to 3 would be retained. In this group are the short-headed *Holodipterus* and *Chirodipterus*, the long-headed *Griphognathus* and possibly *Scaumenacia*. The bone identified as 4 in these genera by Miles (1977) would be T. In a second group of genera, 4 maintained its position and size, ultimately coming into contact with X when T was finally eliminated together with the lateral line to 3. In other words, in this group 4 is the characteristic 4 of *Dipterus*. Along with *Dipterus* in this second group are forms such as *Sagenodus* and *Ctenodus*. We are not suggesting that these groups are monophyletic.

C. australis is of interest in this regard. Miles (1977, p. 230) commented that a canal from 4 to 3 is present in *Holodipterus* and *Griphognathus* and that this 'is surely a primitive dipnoan character'. No mention is made of this canal in *Chirodipterus*. In the ANU collection there are five specimens with bones 3 and 4 preserved, and four of them clearly show a canal passing from 4 to 3. We cannot find it in the fifth. Of the four specimens figured by Miles in which 3 is shown, three have lateral line pits. We conclude that a supraorbital branch from 4 to 3 was normal in *C. australis*, and its apparent absence in two of the nine specimens mentioned above could be the result of a lack of canal definition, or of variation between specimens. His 4 is therefore T.

In summary, we see no reason to accept the unargued and oversimplified statement of Miles that the bone identified by Thomson and Campbell as T in *Dipnorhynchus* is in fact 4, and its corollary that the bone they identified as 4 is in fact 5. There are reasons for believing that a reduction of the cheek bones took place in at least two different ways, and in view of the heterogeneous nature of at least one of the groups of genera defined by these different types of reduction, it seems probable that similar types of reduction took place independently in distantly related taxa.

THE EXTRASCAPULAR SERIES IN DIPNORHYNCHIDS

There has been contention for some time about the normal existence of a bone between Z and A in the extrascapular series of primitive dipnoans. White (1965, p. 26) considered that such a bone was present, and Denison (1968, p. 357) designated it H. Graham-Smith (1978, p. 86) has discussed the matter and has concluded that H probably did not exist in either *Dipnorhynchus* or *Uranolophus*, and Miles (1977, p. 222) makes the odd statement that 'as there is no evidence of such a bone there is no reason to postulate its existence'. On the other hand, Thomson and Campbell (1971) presented evidence that they regarded as indicative of the existence of H in *Dipnorhynchus*. More evidence is now available from *D. kiandrensis* and the new dipnorhynchid genus from Cave Island, referred to above, which has an almost complete posterior edge to the fixed skull roofing bones. The following are the observational data.

(*a*) The space occupied by bone A in *D. sussmilchi* is delineated on 18815 ANU, as shown by Thomson and Campbell. The posterior outlines of the skull of the new dipnorhynchid genus and *Uranolophus* show that A would have occupied a comparable space. Certainly it would not have extended laterally beyond the topographic centre of I.

(*b*) In all three dipnorhynchid specimens and in *Uranolophus*, Y_2 is very transverse in comparison with its homologues in *Dipterus* and later genera. This gives the posterior edges of these skulls an unusually great width, which is emphasized in flattened specimens. Compare, for example, Denison's restorations of the roofs of *Uranolophus* and *Dipterus* (1968, figs. 3*a* and 3*d*). In the primitive genera the width measured from the midline to the extremity of Y_2 around the skull curvature is 41-45% of the total skull length, whereas in *Dipterus* and *Chirodipterus* the figures are 30 and 34% approximately. It is emphasized again that in *Dipnorhynchus*, at least, the skull is not only wide but high. Measured from the level of the palate to the posterior roof crest, the height of the skull in *D. sussmilchi* is *c.* 65% of the skull length as opposed to *c.* 40% in *C. australis* (text-fig. 7).

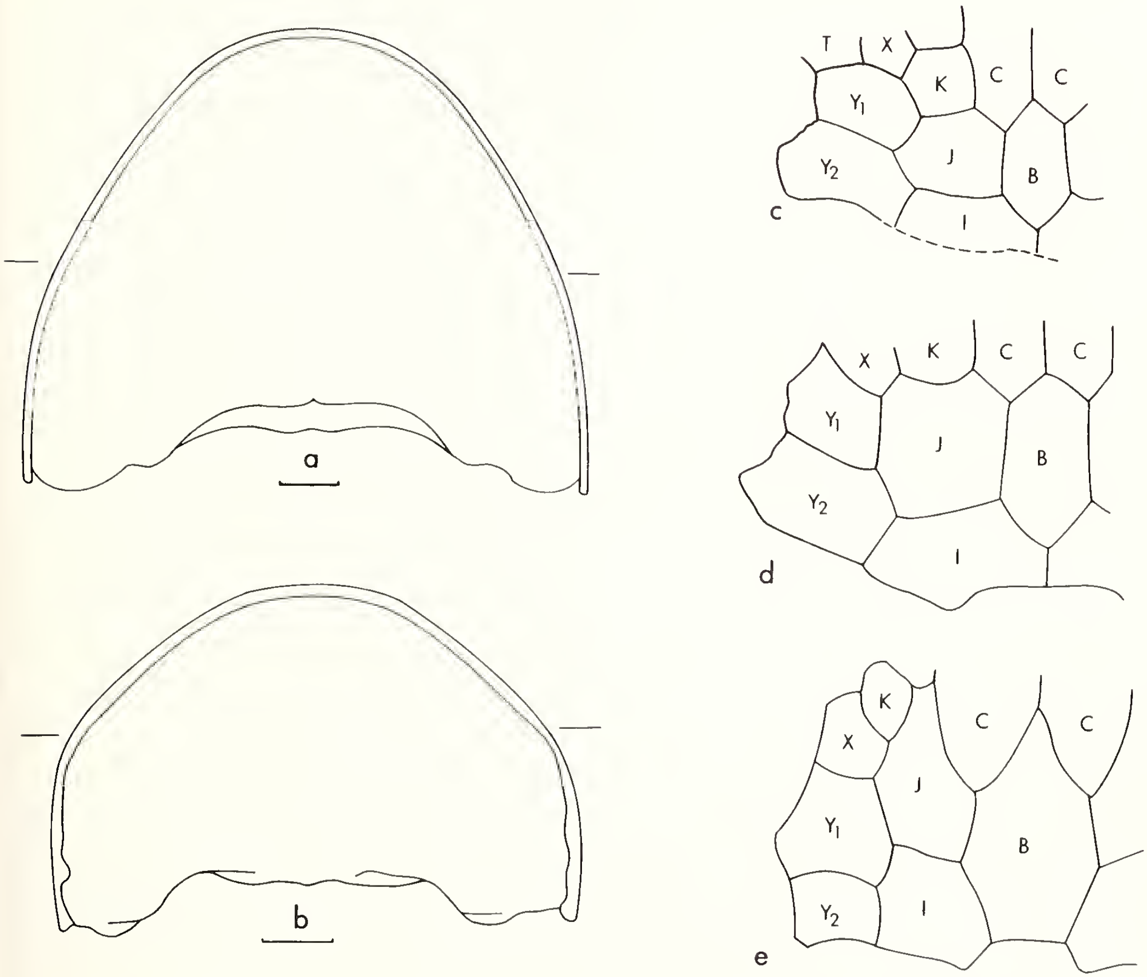
(*c*) The outlines of the posterolateral skull edges on the new genus and *Uranolophus* (Denison, 1968, fig. 3*a*) indicate that Z extended from the edge of Y_2 part way across I, and that a smaller bone lay in an embayment in I between Z and A. Though the edge of I on the *D. kiandrensis* is incomplete, enough of it is preserved to show that the embayment for Z was of the same type. In the ANU specimen of *D. sussmilchi* only the left side is well preserved, and it also shows a similar but weaker embayment.

Of the five new specimens of *C. australis* showing the rear edge of the roof, two are embayed in this position, and one actually shows the bone H between Z and A on one side and a gap in the appropriate place on the other (Pl. 53, fig. 5). This bone does not have the morphology of a scale that extends forwards into the extrascapular series (cf. Miles 1977, p. 222). It is entirely similar to the other extrascapular bones except that it has no lateral line canal. The importance of this is that, despite the fact that though the distance from the outer edge of Z to the outer edge of A is only 22% of the skull length there is a tendency for a bone to develop between Z and A. In *D. sussmilchi* the corresponding figure is 30%, and in *Uranolophus* it is slightly greater.

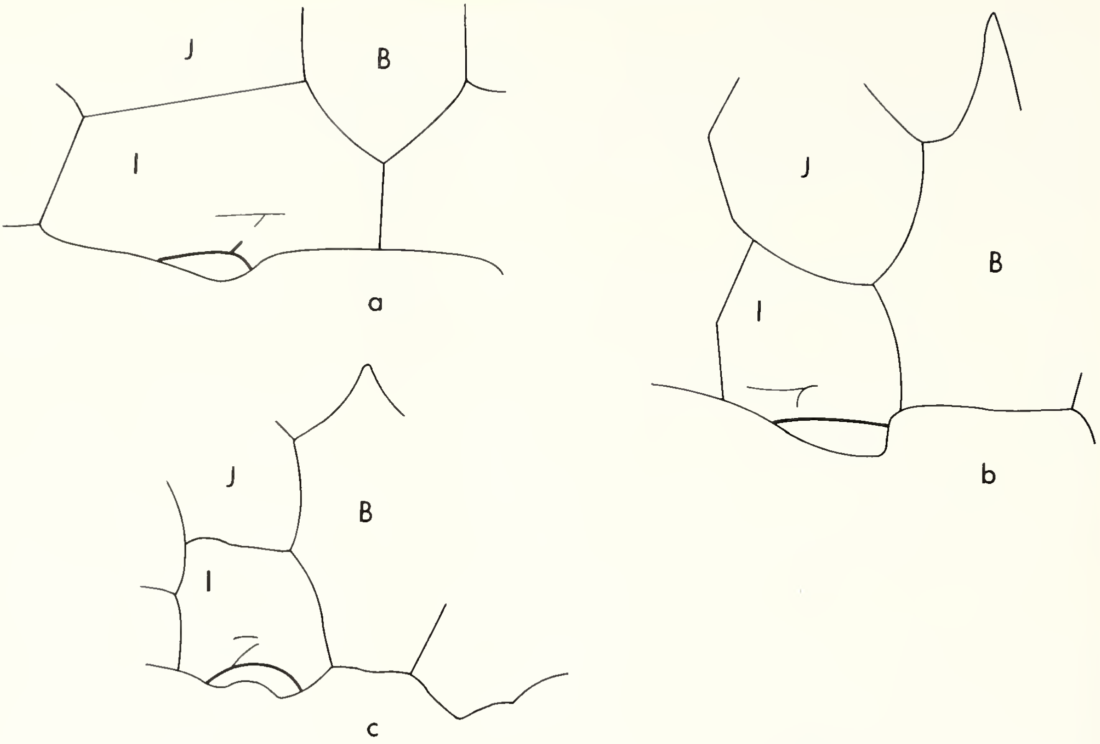
(*d*) We believe that Graham-Smith (1978, p. 86) is in error in stating that 'in *Uranolophus* this part of the skull closely resembles that of *Dipterus*, so that the extrascapular bones, if present, were probably similar'. In the first place, the size of A relative to skull width is much greater in *Dipterus*, as his Figure 21*c* shows. However, his Figure 21*a*, which is based on *Uranolophus* and *Dipnorhynchus*, does not represent either genus in the outline of the posterior edges of Y_2 and I and, assuming that H is not present, the width of Z relative to A is greatly underestimated. He shows $A \simeq Z$ in width, whereas in *Uranolophus* judging from Denison's Figure 3A, A is *c.* 83% of Z, and the corresponding figure for *D. sussmilchi* is *c.* 75%, if there is no H.

(*e*) Further preparation of the ANU specimen of *D. sussmilchi* shows that Thomson and Campbell were in error in concluding that the occipital commissure did not pass through I. In fact it catches the corner of that bone, having a long lateral branch that lies at a high angle to the sagittal line and a shorter median branch turned back sharply to A (Pl. 53, figs. 9–10). At the point of flexure at least one short canal runs towards the ossification centre of I, the main part of the canal passing well behind that centre. The evidence from the new genus from Cave Island is that a canal is present in a similar position, and, although the whole canal has not been directly observed in *Uranolophus*, Denison noted pores on I in two of his specimens and part of a canal in another. It is clear, then, that I was canal-bearing in all three primitive genera known at the present time.

(*f*) In *Dipterus*, *Chirodipterus*, and *Griphognathus* the centre of ossification is displaced well back towards the back of I, and the commissural canal loops forwards towards this centre. So far as we can determine, the canal is embedded in the bone, and does not lie in a spongy tube like the canals under Y_2. The largest specimen of *Chirodipterus* in our collection, however, shows the canal lying in an open slit in the angle between



TEXT-FIG. 7. *a*, Posterior profile of *Dipnorhynchus sussmilchi* and *b*, *Chirodipterus australis* to show relative widths and heights of the skulls. The short horizontal line indicates the lowest extension of Y_2 in each case. *c*, *Dipnorhynchus kiandrensis* sp. nov. *d*, *D. sussmilchi* (18815 ANU), and *e*, *C. australis* (35640 ANU); bones at rear of skulls drawn to same scale and flattened to show relative widths of elements. (Scale = 10 mm.)

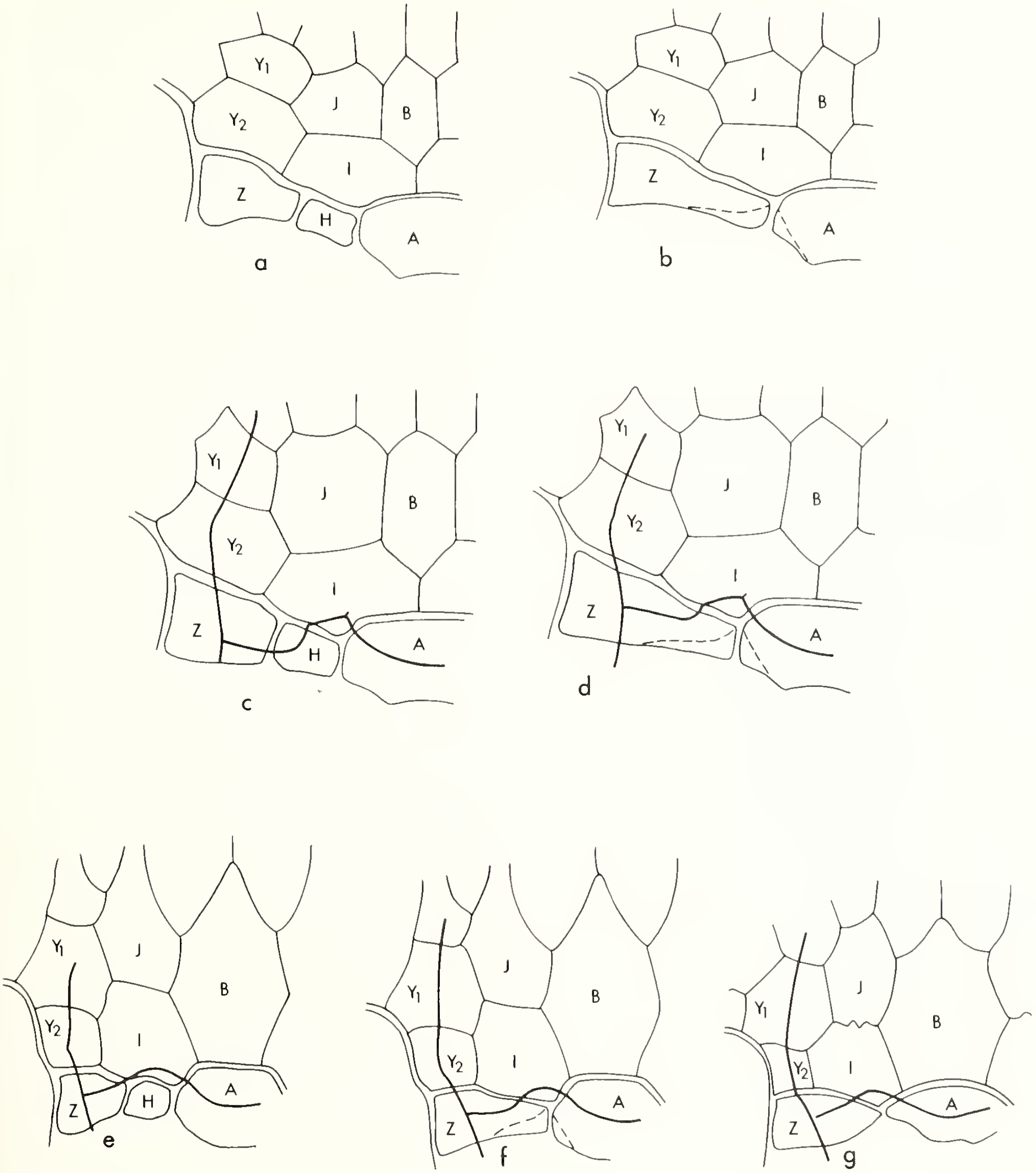


TEXT-FIG. 8. Posteromedial parts of skull roof of *a*, *Dipnorhynchus sussmilchi* (18815 ANU) and *b*, *c*, *Chirodipterus australis* (35639 ANU, and 35640 ANU) to show position of the occipital commissure in I in relation to the pit lines.

the main part of the bone and the posterior horn (Pl. 53, fig. 8). This suggests that some resorption has taken place during growth, allowing the canal to move backwards as the bone increased in size. In this regard, it is of importance that the pit-lines in all these genera, as well as in the dipnorhynchids, lie entirely in front of the canal, and their two branches meet over the ossification centre (text-fig. 8).

It seems to us, therefore, that although no primitive genera have been found with the extrascapular series in place, the available evidence is that there was a bone H which was a normal extrascapular bone. The question now is whether this bone carried the lateral line. There are several lines of evidence supporting the view that it did.

In the first place, the shape of the space for Z in *D. sussmilchi* indicates that Z did not extend to the point where the canal enters I, and therefore must have been carried in H as is shown in text-fig. 9*c*. Secondly, the embayment for A is slight in the primitive genera in comparison with later ones in which a projection from I also tends to divide the extrascapular series, with the result that the canal could more readily pass behind I in the primitive genera. As both White (1965) and Graham-Smith (1978) pointed out, even in *Dipterus* there is a tendency for the canal to pass behind I. And finally, the fact that in all the above-mentioned forms the canal passes behind the ossification centre of I and shows evidence of having moved back in the bone during ontogeny, suggests that it has only moved into I because the bone behind was eliminated (possibly by not only becoming progressively smaller, but also by ossifying progressively later in ontogeny). In this way the neuromasts would become associated with I early in ontogeny (see Graham-Smith, 1978, p. 86).



TEXT-FIG. 9. Left posterior parts of skull roof in *a–b*, *Dipnorhynchus kiandrensis* sp. nov.; *c–d*, *Dipnorhynchus sussmilchi* (18815 ANU); and *e–g*, *Chirodipterus australis*, *e–f*, 35640 ANU, *g*, 35638 ANU. The extrascapular series in *a–b* and *c–d* are hypothetical, but the extrascapular bones have been observed in *e* and *g*. The left-hand figure in each set *a*, *c*, and *e* shows the pattern with H present; *b*, *d*, *f*, and *g* show the pattern without H; the dotted lines on Z and A show alternative bone outlines, like those in *g*.

ROOF OF NASAL CAPSULES

The space between the roof of the nasal capsule and the dermal roofing bones (the ethmoid capsule of the tectum nasi) in *D. sussmilchi* is occupied by a mass of ossified rostral canals (Thomson and Campbell 1971, p. 70) whose distribution had to be examined by X-radiography. Similar canals had been noted in *Chirodipterus wildungenesis* by Säve-Söderbergh (1952), and they have been subsequently observed in detail in *C. australis* and *Griphognathus whitei* by Miles (1977).

In *D. kiandrensis* the perichondral lining of the roof of the nasal capsule has been completely removed on the left side and largely removed on the right, exposing the canals. The whole rostral region in this specimen is similar in proportion to that of *D. sussmilchi.* In particular, the ethmoid capsule is depressed in comparison with that of *C. australis.* The maximum height of the capsule in our specimen is 12% of the skull length in *D. sussmilchi* as compared with 17% in *C. australis*, both specimens measured in the median line.

On each side of the midline there are two symmetrically placed major sets of trunks, each of which repeatedly branches. These major canals all lie more or less at the same level, and are not stacked in tiers as they are in *Chirodipterus.* Though it is not certain, it would seem that the two sets of canals penetrated the post-nasal wall through a single foramen and they correspond with the canals for the r. ophthalmicus profundus V and the r. ophthalmicus superficialis VII in *Chirodipterus.* These canals are the ones labelled *prof. m.* and *prof. l.* by Säve-Söderbergh 1952, fig. 4, and by Miles 1977, fig. 66. We have decided on the above homologies because the median set of canals is swinging sharply laterally towards the posterior as though to make a junction, and because the lateral set lies topographically near the suborbital lateral line canal only at its anterior extremity. Only two other nerves enter the tectum nasi of modern genera, viz. the nasalis externus profundus V and the buccalis lateralis VII. Both of these are closely associated with the suborbital canal, and are situated more laterally than the canals in *D. kiandrensis.*

All the canals consist of a delicate meshwork of bony tissue as is shown on Pl. 52, fig. 6.

In *D. kiandrensis* the major canals diminish only slightly in diameter towards the snout where they pass into the thick spongy rind of bone forming the snout. Presumably some of the canals form tubuli that open through sensory pores as is common in other Devonian dipnoans. However, in addition to these there are vast numbers of finer ramifying tubuli whose function is not clear.

The branching pattern of both major series of canals is shown on Pl. 52, fig. 4. There are numerous connecting canals between the major ones on each side, and across the midline. The connecting canals are finer than the major ones. Most of the connections take place via a layer of delicate canals lying close up under the dermal bones. These connections divide and rejoin to form an anastomosis of increasingly finer canals that become appressed to the inner surface of the dermal bones where they either join with their neighbours or pass through the thin smooth layer of periosteum forming the inner dermal bone surface.

A feature that is probably of significance is that a branch of the median series lies almost along the lateral line canal, and small canals from it ramify over the perichondral layer covering the canal. They pierce it, enter the spongy cover, and then presumably join the canal. Certainly where the inner walls of the canal can be observed in the snout region they are perforated by numerous foramina that represent the entry points of the fine canals.

Another set of canals, much fewer in number, penetrate the roof of the nasal capsule and run anterodorsally to meet those in the ethmoid capsule. Some of these are large, particularly those few tucked under the edge of the lip (cf. those labelled *f.m.* and *f.l.* in *C. australis* by Miles 1977, fig. 64). Presumably they represent the paths of nerves that have passed down from the ethmoid capsule into the nasal capsule, and are re-entering the ventral wall of the ethmoid capsule anteriorly.

A final point is that a set of delicate ramifying canals is attached to the visceral surface of the roofing bones in all areas where the neurocranium covers these bones (Pl. 53, fig. 6). These canals are visible in patches on the present specimen, particularly under L_1, L_2, part of 3, T, Y_2, and I. They have a similar relation to these bones as do the fine canals in the ethmoid cavity to their overlying dermal bones, but apparently they exist only in a plane immediately under the surface of these bones. Laterally they penetrate the neurocranial wall under 3 and T, and open into the orbital chamber (Pl. 53, fig. 6, arrows). The specimen of the new dipnorhynchid genus from Cave Island shows these canals better than the Lick Hole individual. In particular, the outlines of the planum antorbitale and the two walls of the median crista against the dermal roof are well shown, and traces of the tubules are observed extending back medially a long distance behind the pineal foramen.

As indicated above we accept the conventional view that the ethmoid canals carried branches of the ramus ophthalmicus profundus V and the ramus ophthalmicus superficialis VII. However, the shape and distribution of the fine canals, especially the fine anastomosing set, outside the regions where they could be involved with the innervation of either a snout sensory organ or the lateral line system, indicates that they permitted the circulation of fluids from the braincase to and from the dermal bones, and/or that they provided the innervation for the sensory organs that are thought to have filled the fine canal system within the cosmine cover of the dermal bones (Thomson 1977).

Acknowledgements. We wish to acknowledge the gifts of the specimen to the Australian National University by the discoverers, Dr. B. D. E. Chatterton and staff and students of Macquarie University, Sydney. Dr. A. Ritchie and Mr. R. Jones of the Australian Museum, Sydney, made the resin preparation from the original specimen. The X-radiographs were prepared by Mr. W. Ambrose of the Department of Prehistory and Anthropology, Research School of Pacific Studies, A.N.U., and printed by Mr. Ivan Fox, Zoology Department, A.N.U. Mrs. L. Wittig and Mr. L. Seeuwen of the Geology Department, A.N.U., prepared the majority of text-figures and the photographs.

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PALAEOBIOLOGY AND SYSTEMATICS OF LARGE CYCLOSTOME BRYOZOANS FROM THE PLIOCENE CORALLINE CRAG OF SUFFOLK

by PETER S. BALSON *and* PAUL D. TAYLOR

ABSTRACT. Bioclastic sands of the Coralline Crag are characterized by abundant bryozoans including large colonies of four cyclostomes: *Blumenbachium globosum* Koenig, *Meandropora aurantium* (Milne Edwards in Lyell), *M. tubipora* (Busk), and *Multifascigera debenensis* sp. nov. These species are systematically described and the relationships investigated between colony growth pattern, form, and inferred ecology. Colonies of each species are composed of numerous subcolonies bounded by exterior walls. Times of autonomous subcolony growth were punctuated by periods of subcolony anastomosis. Most colonies acquired a roughly hemispherical shape but others developed a subspheroidal form. The former apparently retained a stable attitude during growth whereas the latter either enveloped an unstable substrate (circumrotatory growth) or were attached to a perishable substrate which supported the colony above the sea-bed. Colonies are absent from the turbulent sandwave facies of the Coralline Crag but are present in other facies where mobile animals rather than currents may have been responsible for overturning circumrotatory colonies. Evolution of exterior wall-bounded subcolonies, known in many post-Palaeozoic cyclostomes, was possible because interzooidal pores allowed soft tissue connection between subcolonies beneath the colony surface when soft tissue was absent above it. The localization of coelomic damage may have been a factor in the success of this type of organization.

THE Coralline Crag is a marine Pliocene formation of bioclastic sands and silty sands which has a small outcrop in south-east Suffolk. The Coralline Crag and overlying Plio-Pleistocene Red Crag were originally considered to be parts of a single deposit but in 1835 Charlesworth showed that this was clearly divisible into two. The upper deposit he termed Red Crag after its distinctive coloration because of post-depositional staining by iron oxides. The lower deposit he termed Coralline Crag after the abundance of 'corals', later shown to be the skeletal remains of bryozoans (Wood 1844; Busk 1859). Among the most conspicuous of these bryozoans are the large colonies of four superficially similar species of cyclostome: *Blumenbachium globosum* Koenig, *Meandropora aurantium* (Milne Edwards in Lyell), *M. tubipora* (Busk) and *Multifascigera debenensis* sp. nov. The aim of this paper is to revise the systematics of these species and to explore the relationships between colony growth pattern, form, and inferred palaeoecology. Unless otherwise stated, specimens are held in the palaeontological collections of the British Museum (Natural History).

SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder CERIOPORINA Hagenow, 1851
Family incertae sedis
Genus BLUMENBACHIUM Koenig, 1825

Type species. Blumenbachium globosum Koenig, 1825, by monotypy.

Emended diagnosis. Colony composed of numerous stacked layers of cup-shaped subcolonies

[Palaeontology, Vol. 25, Part 3, 1982, pp. 529-554, pls. 54-56.]

bounded by exterior walls; subcolonies are free proximally but contiguous distally where exterior walls of adjacent subcolonies interdigitate.

Remarks. Blumenbachium Koenig, 1825 and *Alveolaria* Busk, 1859 have the same type species. Therefore, *Alveolaria* is an objective junior synonym of *Blumenbachium*. The only species of *Blumenbachium* which has been described is *B. globosum* from the Coralline Crag. Lonsdale in Murchison (1839) and d'Orbigny (1850) used *Blumenbachium* incorrectly when referring to small discoidal bryozoans of Silurian age.

Familial assignment of *Blumenbachium* remains in doubt and, indeed, its subordinal assignment to the Cerioporina must be considered tentative until the cerioporinids as a group are better understood.

Blumenbachium globosum Koenig, 1825

Plate 55, figs. 5, 6; Plate 56, figs. 1, 3, 4; text-figs. 1, 2, 5, 7, 8

1825 *Blumenbachium globosum* Koenig, p. 3, pl. 5, fig. 69.
?1844 *Theonoa*(?) *globosa* Wood, p. 13.
1859 *Alveolaria semiovata* Busk, p. 128, pl. 19, fig. 4; pl. 21, fig. 3.
1889 *Alveolaria semiovata* Busk; Nicholson and Lydekker, p. 620, fig. 463.
1922 *Alveolaria semiovata* Busk; Canu and Bassler, p. 111, fig. 32, pl. 18, figs. 1–4.
1948 *Alveolaria semiovata* Busk; Chatwin, fig. 17, 12.
1952 *Alveolaria semiovata* Busk; Lagaaij, p. 185, pl. 26, fig. 2.
1953 *Alveolaria semiovata* Busk; Bassler, p. G70, fig. 35, 5.
1957 *Alveolaria semiovata* Busk; Buge, p. 116, pl. 5, fig. 6.

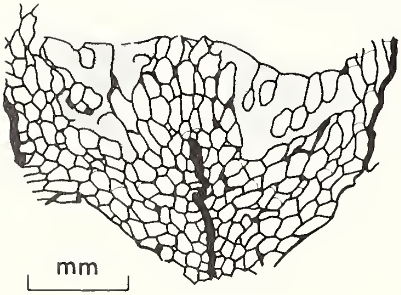
Lectotype. D 52755 'White Crag, Suffolk'. C. Koenig Collection. Figured by Koenig (1825, pl. 5, fig. 69 lower colony).

Paralectotype. D 52754 'White Crag, Suffolk'. C. Koenig Collection. Figured by Koenig (1825, pl. 5, fig. 69 upper colony).

Other material. Coralline Crag, Suffolk: 8814, 23474, 51157, 60209, 60479, B 1385 (described by Smith 1817), B 1704, B 1712, B 4290, B 4308, B 4311, D 1495, D 6902–4, D 6905 (lectotype of *Alveolaria semiovata* Busk, 1859 chosen by Lagaaij 1952), D 51067–70, D 52767–8, D 52773–4, D 53128–31, Sedgwick Museum (Cambridge) C 50972.

Description. Colonies vary in shape from roughly spheroidal (Pl. 56, fig. 1) to hemispherical (Pl. 55, fig. 6), and are composed of numerous radially arranged subcolonies, each bounded laterally by an exterior wall. Subcolonies are free proximally but are contiguous and generally six-sided distally where their bounding exterior walls are convoluted and interdigitate with those of adjacent subcolonies (text-fig. 5). The united edges of adjacent subcolonies stand out as ridges, bisected by the protuberant juxtaposed exterior walls, forming a polygonal network on the zoarial surface (text-fig. 7). New generations of subcolonies arise from the surface of earlier subcolonies. In section, colonies are concentrically layered, each layer consisting of a single generation of united subcolonies (text-fig. 8).

Zooecia were budded by division of existing interzooecial walls on subcolony-bounding exterior walls (acting as budding laminae), and interzooecially (see McKinney 1975) by interzooecial wall division at triple junctions between established zooecia. Zooecia are tubular and polygonal in cross-section. They are occasionally divided by one or more subterminal diaphragms (see Nye 1968), convex distally (text-fig. 1), and sometimes



TEXT-FIG. 1. *Blumenbachium globosum* Koenig, D 6905. Drawing of a thin section through a brood chamber (stippled). Pendant-like structures (right of centre) are autozooecia supported within the chamber by interior walls. Curved walls projecting into chamber (left of centre) may be interior walls partially resorbed during brood chamber formation. Thin, convex upwards walls partitioning some autozooecia are interpreted as subterminal diaphragms.

closed by a terminal diaphragm. The polygonal apertures of mature zooecia average about 0·11 mm in width. Distinction between autozooecia and any kenozooecia is unclear although some colony surfaces exhibit longitudinal rows of relatively large, slightly protuberant, open zooecia (probably autozooecia) separated from one another by rows of smaller zooecia (possibly kenozooecia) which are characteristically occluded by convex diaphragms. Structures resembling lunaria occur in a few colonies. Brood chambers are rare but when present are extensive and occupy the depressed centre of the cup-shaped subcolonies. The roof of the brood chamber is a thin ?exterior wall pierced by scattered autozooecia, typically occluded by terminal diaphragms (text-fig. 2A). Together with interior walls, these zooecia divide the brood chamber internally (text-fig. 1). Ooeciopores have not been positively identified.

Remarks. This species is often referred to as *Alveolaria semiovata* Busk, 1859, but Koenig's first description of *Blumenbachium globosum* in 1825 predates that of *Alveolaria semiovata.* The name *Blumenbachium globosum* was later used by Prestwich (1871, p. 123) and is here revived for this common Coralline Crag fossil. A lectotype (Pl. 56, fig. 1) and a paralectotype have been chosen from Koenig's syntypes which clearly match his illustrations.

Prior to Koenig's publication, Sowerby (1804–1817) figured *B. globosum* (pl. 481, lower figure) describing it as 'a sort of *Millepora*'. The first of the unnamed Crag 'zoophytes' described by William Smith (1817) is also *B. globosum* (specimen B 1385), as is the bryozoan illustrated by R. C. Taylor (1830, fig. 65*a*, *b*) also described as a 'crag zoophyte'.

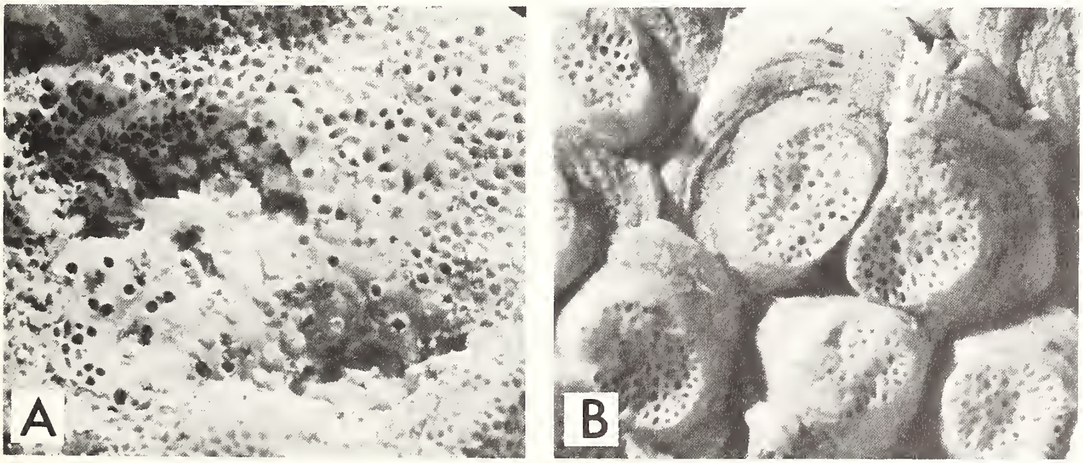
Stratigraphical occurrence. Pliocene: Coralline Crag (Gedgravian) of Suffolk, England; Scaldisian of the Scheldt Estuary, Holland (Lagaaij 1952); Redonian of Saint-Denis-d'Oleron, France (Buge 1957).

B. globosum also occurs as a derived fossil in Plio-Pleistocene deposits, notably the Red Crag of East Anglia.

Suborder TUBULOPORINA Milne Edwards, 1838
Family FRONDIPORIDAE Busk, 1875
Genus MEANDROPORA d'Orbigny, 1849

Type species. Fascicularia aurantium Milne Edwards *in* Lyell 1838.

Emended diagnosis. Frondiporidae with large colonies composed of radiating, cylindrical fascicles of elongate zooids which divide and anastomose at intervals.



TEXT-FIG. 2. *Blumenbachium globosum* Koenig. A, surface of a brood chamber pierced by circular autozooecial apertures some of which are occluded, B 1704, Coralline Crag, Sutton, ×13. B, cup-shaped subcolonies on the underside of a fractured specimen, D 1495, Coralline Crag, Suffolk, ×12.

Remarks. Meandropora was established by d'Orbigny in 1849 to replace the *Fascicularia* of Milne Edwards (in Lyell 1838) which is not the same as that of Lamarck (1812). Three species of *Meandropora* are generally recognized: *M. aurantium* (Milne Edwards in Lyell 1838), given as the type species by d'Orbigny (1849), *M. tubipora* (Busk 1859), and *M. cerebriformis* (de Blainville 1830). The first two species occur in the Coralline Crag and are described below. *M. cerebriformis* is characterized by a meandroid pattern of fascicles on the colony surface (see Buge 1948, pl. 7, figs. 3–4).

Meandropora aurantium (Milne Edwards in Lyell, 1838)

Plate 54, figs. 5, 6; Plate 55, fig. 1; Plate 56, figs. 2, 6, 7

1838 *Fascicularia aurantium* Milne Edwards [sp. nov.]; Lyell, p. 303, fig. 133.
1844 *Fascicularia aurantium* Milne Edwards; Wood, p. 13.
1859 *Fascicularia aurantium* Milne Edwards; Busk, p. 131, pl. 21, fig. 3.
1890 *Fascicularia aurantium* Milne Edwards; Reid, fig. 3.
1948 *Theonoa aurantium* (Milne Edwards); Chatwin, fig. 17, 10.
1952 *Meandropora aurantium* (Milne Edwards); Lagaaij, p. 178, pl. 23, fig. 4.
1957 *Meandropora aurantium* (Milne Edwards); Buge, p. 102, pl. 5, figs. 3, 4.
?1963 *Meandropora aurantium* (Milne Edwards); Malecki, p. 79, pl. 8, fig. 10.

Type. The location of the figured type specimen is unknown and it may be lost. However, as the identity of the species is in no doubt, circumstances do not warrant the designation of a neotype.

Material. Coralline Crag, Suffolk: 8792, 8802, 8812–13, 8845–8, 40034, B 1384 (described by Smith 1817), B 1664, B 3828, B 4294, B 4306, B 4311, D 2079, D 6671, D 6906, D 52765–6, D 52769, D 52775, Sedgwick Museum (Cambridge) C 51082, C 51085.

Emended diagnosis. Meandropora with fascicles of subcircular cross-section, generally dividing and anastomosing at irregular intervals.

Description. Colonies are spheroidal (Pl. 56, fig. 2) subspheroidal, or hemispherical (Pl. 56, fig. 6) and composed of numerous radially arranged, elongate fascicles of zooecia subcircular in cross-section. Their bounding exterior walls may be ornamented by the longitudinal traces of interzooecial walls and occasional growth lines transverse to fascicle length. Division and anastomosis of fascicles generally occurs at irregular intervals, although phases of extensive fascicle anastomosis in some colonies gives rise to solid concentric bands of zooecia (Pl. 56, figs. 6, 7) with little interfascicular space (Pl. 54, fig. 5).

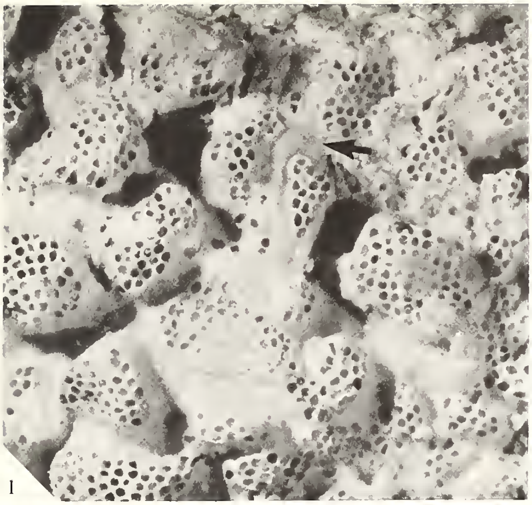
Zooecia open at the distal ends of fascicles (Pl. 54, fig. 6) and were budded by interzooecial division (McKinney 1975) of existing walls within the axial regions of the fascicles. Termination of zooecia usually occurs where they meet the bounding wall of the fascicle after divergence from the centre of the fascicle. More rarely, groups of zooecia are capped by terminal diaphragms following fascicle anastomosis. Zooecia are very long (> 5 mm), thin-walled and polygonal in cross-section. Some zooecia are partitioned by thin diaphragms (?basal diaphragms of Nye 1968) which may be located at the same level in adjacent zooecia. Apertures of mature zooecia average about 0·24 mm in width. Kenozooecia are not evident.

EXPLANATION OF PLATE 54

Figs. 1–2. *Multifascigera debenensis* sp. nov. D 52760, holotype, Coralline Crag, Ramsholt Cliff. 1, typical appearance of colony surface with an inflated gonozooid (arrowed) between autozooidal fascicles, ×9. 2, single subcolony with stellate pattern of fascicles, ×12.

Figs. 3–4. *Meandropora tubipora* (Busk). 3, columnar fascicles arising from discontinuous platform composed of occluded ?kenozooids, D 46751, Coralline Crag, near Sudbourne, ×9. 4, broken ovicell (arrowed) extending between fascicles, D 53154, Coralline Crag, Broom Hill, ×9.

Figs. 5–6. *Meandropora aurantium* (Milne Edwards in Lyell). 5, anastomosed fascicles giving a high density of apertures on colony surface, B 4311, Coralline Crag, ×9. 6, inflated ovicell frontal wall (arrowed) and incomplete ovicells present within fascicles as large apertures, D 52769, Coralline Crag, Aldeburgh Hall, ×11.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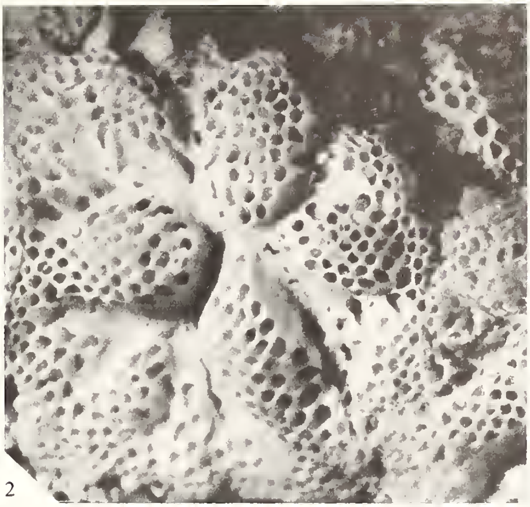
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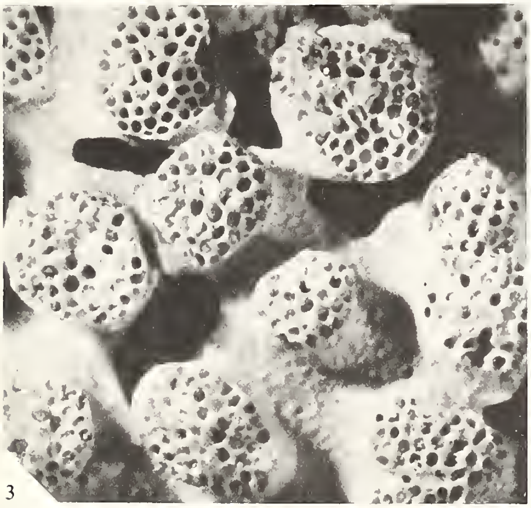
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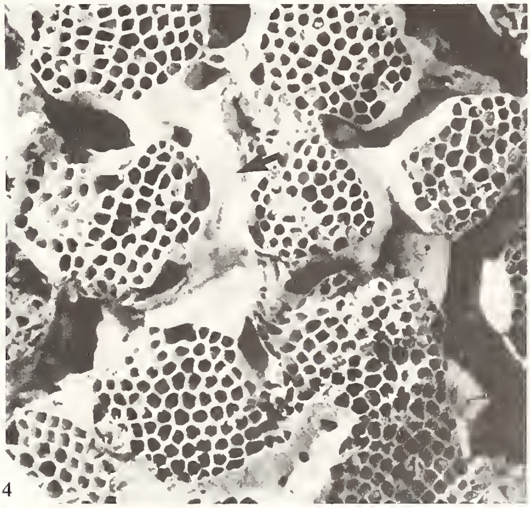
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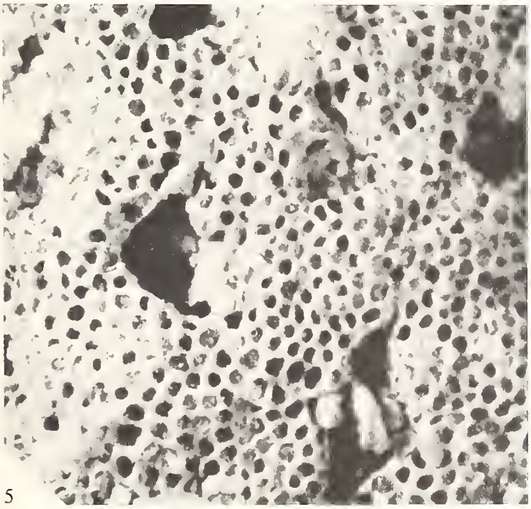
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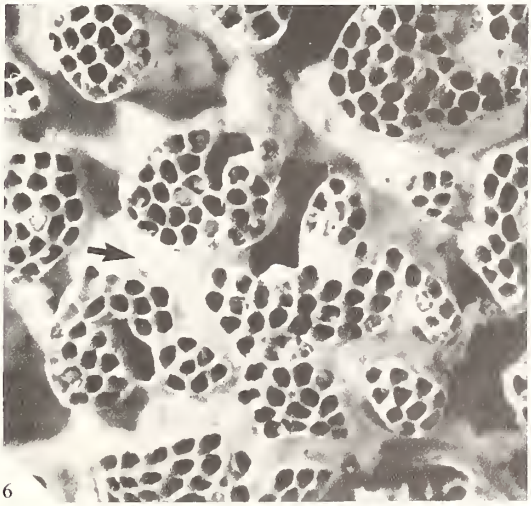
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BALSON and TAYLOR, Pliocene bryozoans

Ovicells occur in a small minority of colonies and are large chambers, possibly originating from a single zooecium, which span the gaps between adjacent fascicles and have thin roofs of exterior wall (Pl. 54, fig. 6). Fascicle diameter is diminished when ovicells are present. Occasional solitary zooecia, circular in cross-section, penetrate the ovicells and are usually occluded by terminal diaphragms. Ooeciopores are difficult to distinguish, although an occluded aperture (*c.* 0·11 mm in width and transversely elliptical) protruding through the frontal surface of one ovicell may be an ooeciopore.

Remarks. Meandropora aurantium was first named when figured as *Fascicularia aurantium* Milne Edwards by Lyell in his *Elements of Geology* (1838). Prior to this, the species was the second of two unnamed 'zoophytes' described by William Smith (1817). Chatwin (1948) incorrectly referred *M. aurantium* to the genus *Theonoa* (type species *T. chlatrata* Lamouroux from the Jurassic) which consists of small discoidal encrusting colonies with radiating linear fascicles of zooecia.

Stratigraphical occurrence. Pliocene: Coralline Crag (Gedgravian) of Suffolk, England; Scaldisian of Wilmarsdonck, Holland (Lagaaij 1952); Redonian of Chalonnes and Sceaux-d'Anjou, Maine-et-Loire, France (Buge 1957). *M. aurantium* also occurs as a derived fossil in the Plio-Pleistocene Red Crag of East Anglia.

Meandropora tubipora (Busk, 1859)

Plate 54, figs. 3, 4; Plate 55, fig. 2; Plate 56, fig. 5

1859 *Fascicularia tubipora* (n. sp.); Busk, p. 130, pl. 21, fig. 1.
1859 *Fungella multifida* (n. sp.); Busk, p. 119, pl. 17, fig. 4.
?1887 *Fascicularia tubipora* Busk; Waters, p. 344.
1952 *Meandropora tubipora* (Busk); Lagaaij, p. 179, pl. 24, fig. 1.
1959 *Meandropora tubipora* (Busk); British Museum (Natural History), pl. 31, fig. 1.

Lectotype (here designated). B 4299 Coralline Crag, Suffolk. This is the specimen figured by Busk (1859) as pl. 21, fig. 1*b*.

Other material. Coralline Crag, Suffolk: 8799, 8801, 8814, 48711, 60207, 60478, B 1667, D 6679, D 46751, D 52770, D 52772, D 53133–4.

Emended diagnosis. Meandropora with fascicles which anastomose at regular intervals to form platforms transverse to colony growth direction.

Description. Hemispherical to spheroidal colonies composed of radiating fascicles of zooecia which anastomose with adjacent fascicles at regular intervals to form platforms (Pl. 55, fig. 2). New generations of fascicles arise from the platforms between areas composed of occluded zooecia (?kenozooecia); fascicles are subcircular in cross-section and have slightly domed distal growing surfaces. Exterior walls bounding fascicles are commonly ornamented by longitudinal traces of interzooecial walls and may bear faint growth lines.

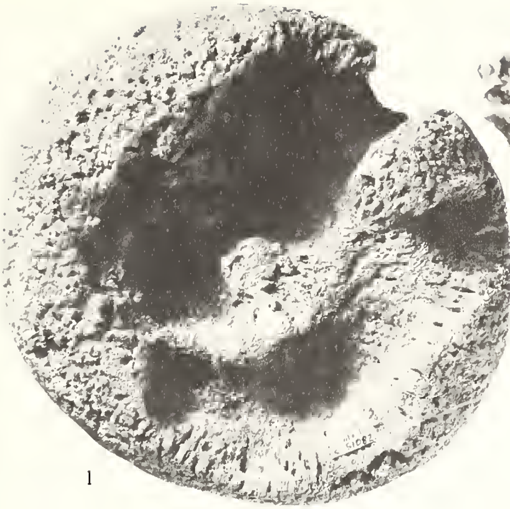
EXPLANATION OF PLATE 55

Fig. 1. *Meandropora aurantium* (Milne Edwards in Lyell), colony with large basal hollow which may have served as a crab domicile, Sedgwick Museum C 51082, Coralline Crag, Broom pit, Gedgrave, ×0·75.

Fig. 2. *Meandropora tubipora* (Busk), fascicles with uniting platforms, D 52772, Coralline Crag, Aldeburgh Brick Works, ×3·7.

Figs. 3–4. *Multifascigera debenensis* sp. nov. Coralline Crag, Ramsholt Cliff. 3, large fractured colony, paratype, D 52761, ×0·6. 4, concentric layers of zooecial fascicles, holotype, D 52760, ×4.

Figs. 5–6. *Blumenbachium globosum* Koenig. 5, ridged colony surface with overgrowing cheilostomes (top and bottom right) and serpulid (right centre) which is gradually being covered by further bryozoan growth, D 52773, Coralline Crag, Crag Pit Nursery, ×5·5. 6, sectioned colony attached to a celleporid cheilostome itself encrusting a bivalve (represented by a mould, bottom right), D 52774, Coralline Crag, Aldeburgh Hall, ×0·9.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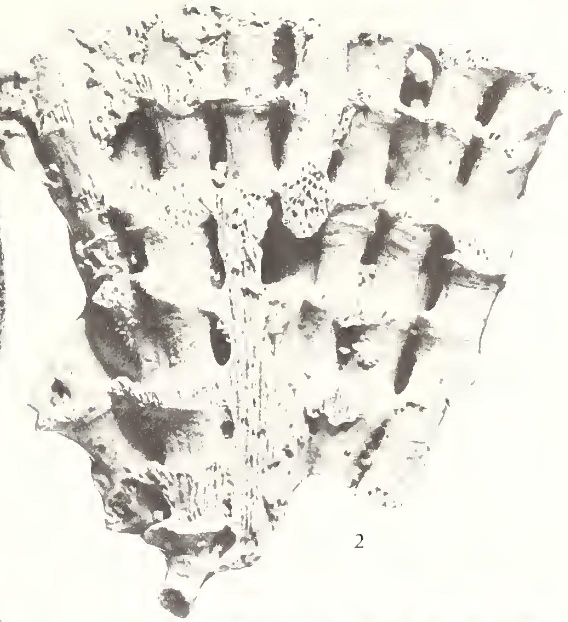
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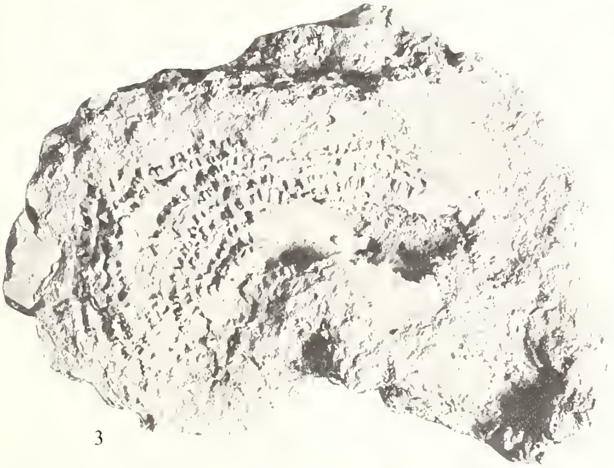
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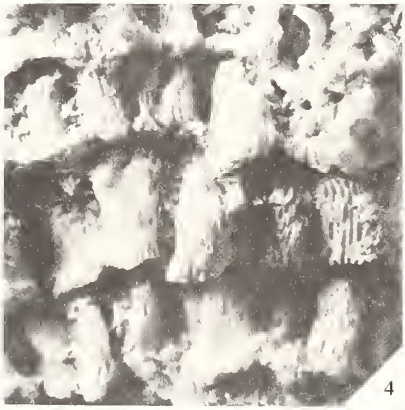
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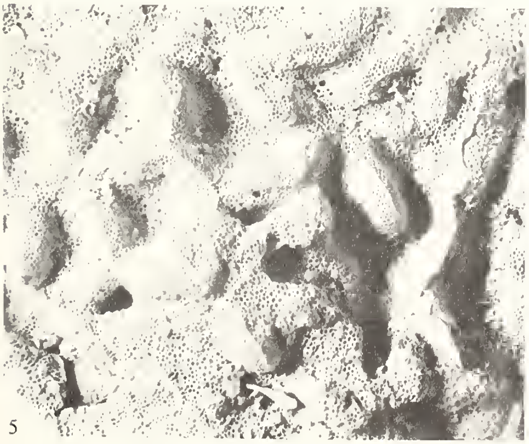
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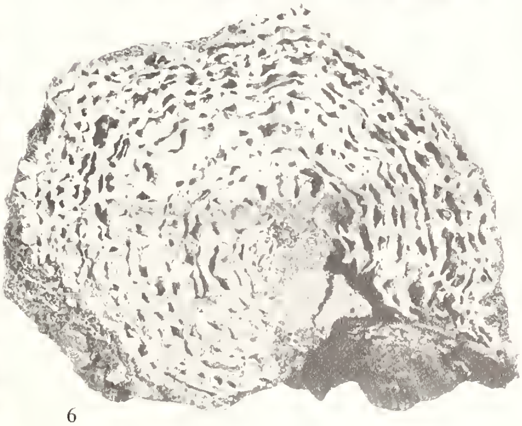
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BALSON and TAYLOR, Pliocene bryozoans

Zooecia are thin-walled and polygonal in cross-section (commonly six-sided) and were budded either interzooecially (McKinney 1975) within fascicles or on the budding lamina formed by the outwardly spreading exterior walls of anastomosing fascicles. Apertures of mature zooecia average about 0·20 mm in diameter. Inferred autozooecia forming the fascicles are very long. Possible kenozooecia (Pl. 54, fig. 3) forming the platforms between fascicles are short (< 1 mm) and are occluded by terminal diaphragms situated slightly beneath the level of the aperture.

Ovicells are uncommon and consist of extensive, irregular chambers (Pl. 54, fig. 4) attached to the exteriors of fascicles and seemingly arising from the platforms between fascicles. They may be partitioned by interior walls and penetrated by zooecia which support their thin pseudoporous roofs. Ooeciopores have not been positively identified.

Remarks. Busk's species *Fascicularia tubipora* was first referred to the genus *Meandropora* by Lagaaij (1952). Following an initial suggestion by Busk, Lagaaij considered *Fungella multifida* Busk, 1859 to be a juvenile stage of *Meandropora tubipora* and this opinion is adhered to here.

An unnamed 'zoophyte' illustrated by R. C. Taylor (1830, figs. 63, 64) is undoubtedly *M. tubipora*. Waters (1887) described a fossil which he referred to *M. tubipora* from the Pliocene of Napier, New Zealand. He also mentioned the occurrence of this species in the Pliocene of Ranetto, Sicily, and in Recent seas. However, these records have not been confirmed and, in the absence of illustrations, may be considered doubtful.

Although closely similar to *M. aurantium* in overall colony form, *M. tubipora* does differ in an aspect which would have been sufficient for Borg (1926, pp. 477–478) to have placed the two species in separate families. Borg considered fasciculate tubuloporinids with fascicles isolated by occlusion of zooecia between them (e.g. *M. tubipora*) to belong to the family Fasciculiporidae, and taxa with 'primary' fascicles (e.g. *M. aurantium*) to belong to the family Frondiporidae. The validity of this opinion cannot be assessed until cyclostome morphology is more clearly understood.

Stratigraphical occurrence. Pliocene: Coralline Crag (Gedgravian) of Suffolk, England.

Family THEONOIDAE Busk, 1859

Genus MULTIFASCIGERA d'Orbigny, 1853

Multifascigera debenensis sp. nov.

Plate 54, figs. 1, 2; Plate 55, figs. 3, 4

Derivation of name. The river Deben on whose banks the bryozoan is found.

Holotype. D 52760 Coralline Crag, Ramsholt Cliff (TM 298428), Suffolk.

Paratypes. D 52761–4 Coralline Crag, Ramsholt Cliff.

Diagnosis. Colony composed of numerous concentric layers of subcolonies united at their edges, each subcolony with a stellate pattern of zooecial fascicles; gonozooecia are interfascicular.

Description. Colonies are large, concentrically layered and tabular, hemispherical or spheroidal in shape (Pl. 55, fig. 3). Each concentric layer (Pl. 55, fig. 4) consists of numerous cup-shaped subcolonies united at their edges. Subcolonies are polygonal in plan view and have a stellate pattern of radiating fascicles on their upper surfaces (Pl. 54, fig. 2). Fascicles tend to have a rounded quadrate cross-sectional shape and their bounding exterior walls may be marked by longitudinal traces of interzooecial walls between slightly convex zooecia. Fascicles diverge obliquely upwards from the centre of the subcolonies and bend until their long axes become orientated almost at right angles to the layering of the colony. A minority of fascicles then expand outwards, overarching non-expanding fascicles, anastomosing with adjacent expanding fascicles, and forming a new concentric layer of subcolonies, each new subcolony being derived from a single expanding fascicle. Concentric wrinkles transverse to growth direction ornament the exterior wall on the undersides of subcolonies.

Zooecia open at the distal ends of fascicles. They were budded by division of interzooecial walls on the budding lamina of exterior wall forming the undersurface of the subcolonies. Zooecia are long, polygonal in cross-section, thin-walled (*c.* 0·01 mm) proximally (near the base of the subcolony), and thicker walled (*c.* 0·02 mm) distally (within the lengthening fascicle). Apertures of mature zooecia average about 0·16 mm in diameter.

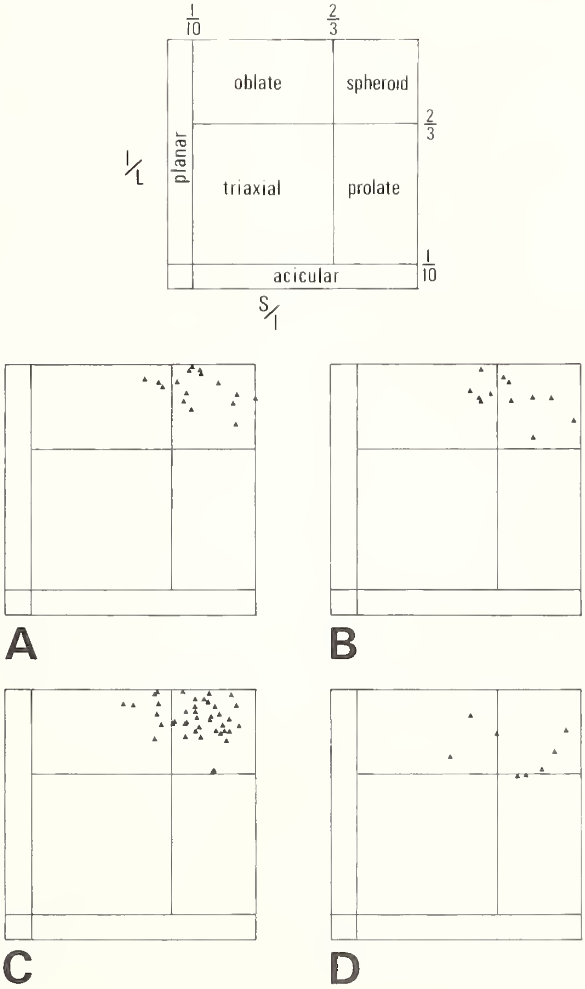
Gonozooecia are rare, interfascicular, and apparently irregular in shape (Pl. 54, fig. 1). Ooeciopores have not been positively identified.

Remarks. Multifascigera debenensis resembles the *Buskia tabulifera* described by Reuss (1864, p. 64, pl. 8, figs. 1–4) from the German Oligocene but has fewer fascicles per subcolony and a tighter packing of subcolonies. *Buskia* Reuss, 1864 is a junior homonym of *Buskia* Alder, 1857, a Recent ctenostome bryozoan. This new Coralline Crag species is most appropriately referred to *Multifascigera* d'Orbigny, a genus previously recognized only in the Cretaceous. The type species of *Multifascigera, M. campicheana* d'Orbigny 1853, has been redescribed by Walter (1972). Assignment of *Multifascigera* to the family Theonoidae is due to the morphological similarity between the subcolonies of this genus and single colonies of *Theonoa.*

Stratigraphical occurrence. The species has been found only in facies A (see facies descriptions below) of the Coralline Crag (Gedgravian) at Ramsholt Cliff.

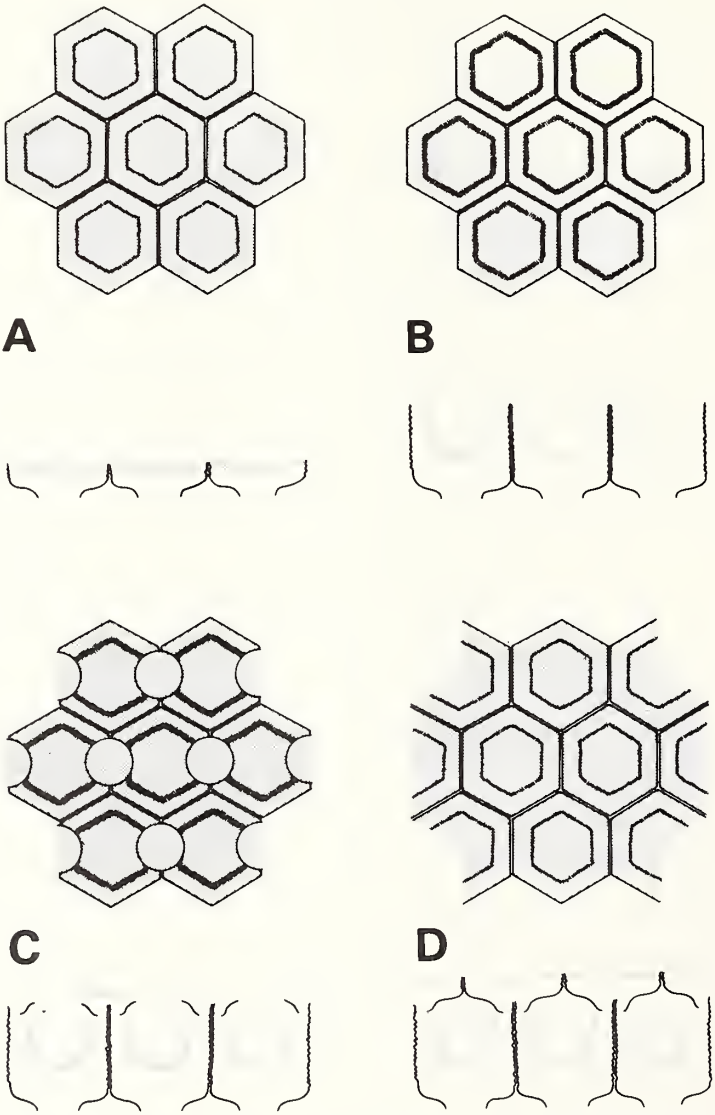
COLONY GROWTH PATTERNS

The overall shape of the colony is broadly similar in all four species. Colonies are usually spheroidal to oblate spheroidal, less commonly hemispherical or tabular. Colony shape has been quantified in a sample of complete colonies and its variation is illustrated in text-fig. 3 using Zingg plots (modified after Folk 1974). Most colonies have a long axis between about 4 and 8 cm long, although some colonies of *Meandropora aurantium* measure up to 16 cm in diameter.



TEXT-FIG. 3. Zingg plots illustrating shape variation among large cyclostome colonies from the Coralline Crag. The upper diagram shows shape nomenclature determined by plotting axial dimension ratios (S = short axis, I = intermediate axis, L = long axis). A, *Meandropora aurantium* (Milne Edwards in Lyell), 16 colonies from Aldeburgh. B, *Meandropora tubipora* (Busk), 12 colonies from Aldeburgh. C, *Blumenbachium globosum* Koenig, 40 colonies from Aldeburgh and Iken. D, *Multifascigera debenensis* sp. nov., 8 colonies from Ramsholt.

The majority of colonies grew radially outwards from an origin situated close to the centre of an encrusting base. A minority of colonies have their origin situated within the core of the colony (see below). In both cases, however, growth was achieved by extension, division, and anastomosis of distinct groups of zooecia comprising subcolonies. This style of colony growth is common to all four species from the Coralline Crag but there are significant differences in the precise pattern



TEXT-FIG. 4. Four stage (A–D) model of colony growth pattern in *Blumenbachium globosum* Koenig. The top diagram for each growth stage shows the colony surface, the bottom diagram is a vertical section. Exterior walls are shown by solid black lines (areas enclosed by exterior walls are subcolonies), inferred hypostegal coelom is stippled, and the steep sides of the ridges around the edges of subcolonies are hatched. Explanation of sequence of events is in the text.

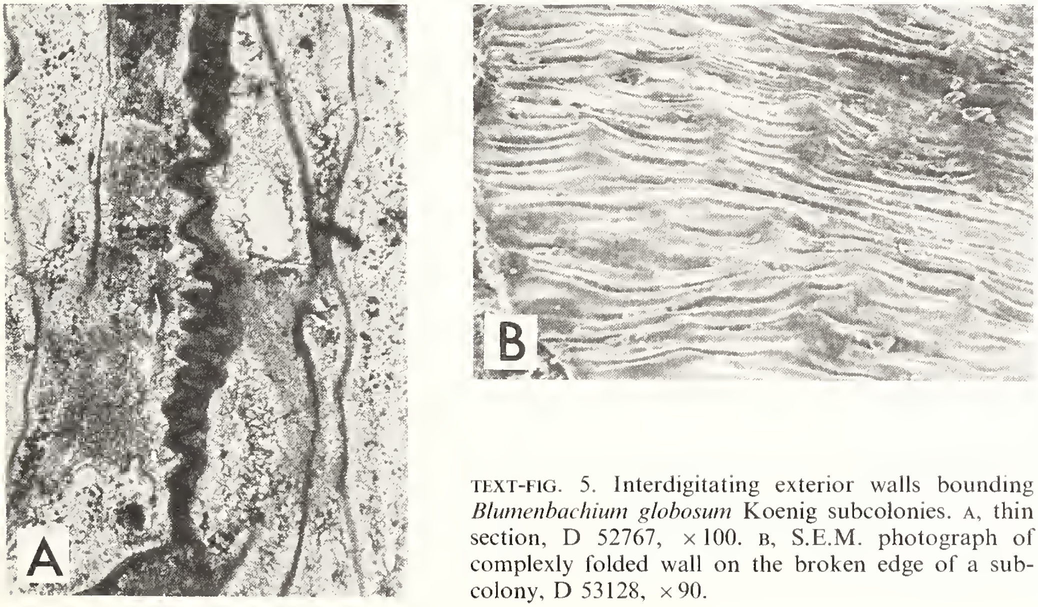
of growth between the species. Colony growth patterns and inferred processes of growth are described below with the aid of simplified diagrams (text-figs. 4, 9–11) depicting geometrically 'ideal' colonies and eliminating zooecial details and incidental irregularities.

Blumenbachium globosum

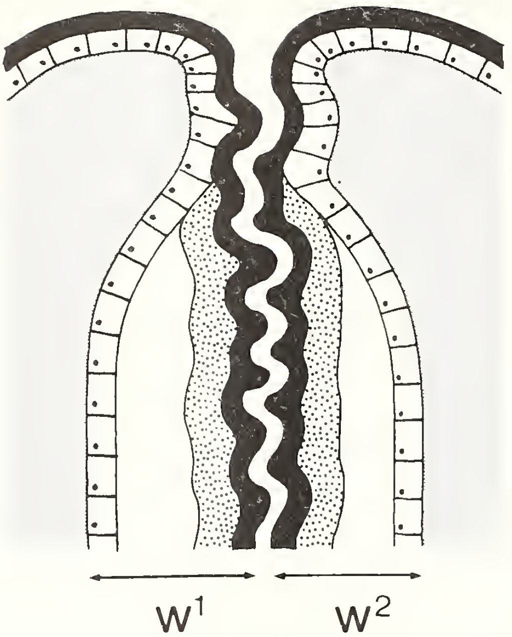
Early colony development has not been studied; early growth stages are often not preserved or are difficult to identify in large and complex colonies.

Text-figure 4 is a model illustrating growth in a portion of an idealized mature colony. The initial surface view (text-fig. 4A) shows seven subcolonies, three of which are cut medially by the diagrammatic section. Each subcolony is bounded by a wall inferred to be a calcified exterior wall, i.e. a calcified wall with an external cuticular layer situated at the colony: environment interface (Boardman and Cheetham 1973). Exterior walls of adjacent subcolonies are juxtaposed and interdigitate with one another to form a complex suture (text-fig. 5). A brown layer, probably representing cuticular remnant (intercalary cuticle), is commonly situated between these adjacent calcitic walls. Tavener-Smith (1975, text-fig. 1) has previously illustrated this structure and his diagram implies that the two interdigitating walls were exterior walls rather than interior walls. Interdigitation of exterior walls does not appear to have been described from a cyclostome bryozoan before, although exterior walls bounding individual zooids are well known to interdigitate in certain cheilostome bryozoans (Banta 1977). The probable distribution of soft tissues in the vicinity of subcolony boundaries in *Blumenbachium* is shown in text-fig. 6.

Upper surfaces of subcolonies are composed of open zooecia of polygonal section. The presence of exposed interzooecial walls indicates that these surfaces were probably enveloped beneath hypostegal coelom during colony life (cf. Boardman and Cheetham 1973, fig. 8). They would have been part of a 'common bud' (*sensu* Borg 1926) within which existing zooecia could have been lengthened and new zooecia budded. Each subcolony would have possessed a separate hypostegal coelom extending as far as the exterior wall bounding the subcolony (text-fig. 4A). Small, newly budded zooecia are concentrated in zones immediately adjacent to the subcolony-bounding exterior walls. These walls evidently functioned as sites of zooecial budding (budding laminae), although zooecial buds also arose in smaller numbers elsewhere on the upper surfaces of the subcolonies.



TEXT-FIG. 5. Interdigitating exterior walls bounding *Blumenbachium globosum* Koenig subcolonies. A, thin section, D 52767, ×100. B, S.E.M. photograph of complexly folded wall on the broken edge of a subcolony, D 53128, ×90.



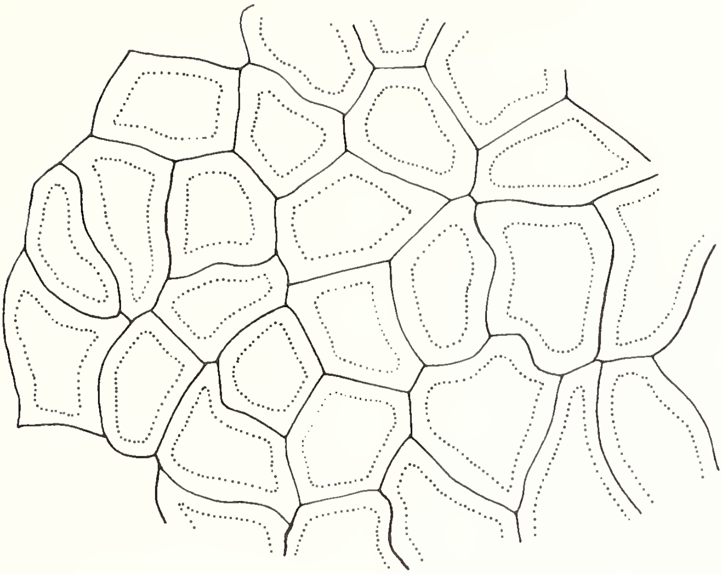
TEXT-FIG. 6. Reconstructed vertical section through the growing edge at the boundary between two contiguous subcolonies of *Blumenbachium globosum* Koenig. Inferred exterior walls bounding the two subcolonies are labelled W^1 and W^2. Each consists of a cuticular layer (solid black), a primary calcified skeletal layer (coarse stipple), a secondary calcified skeletal layer (unshaded), and an epithelial layer (nucleate rectangular cells). Hypostegal coelom is shown by fine stippling. The gap between interdigitating cuticles is exaggerated.

Concentration of zooecial budding and growth close to the peripheries of the subcolonies gave the subcolonies slightly raised edges (text-fig. 4A) which were usually accentuated during subsequent colony growth until they became distinct ridges (text-fig. 4B). Fossils are frequently found with prominent ridges on the colony surface (Pl. 55, fig. 5).

The next stage of growth involved the formation of a new generation of subcolonies on the upper surface of the colony. An initially short and curved length of exterior wall appears to have arisen from the distal ends of interzooecial walls (cf. Taylor 1978, text-fig. 8). Both ends of this wall gradually extended laterally until they joined thus isolating a subcircular patch of zooecia from the surrounding zooecia (text-fig. 4C). Zooecia within this exterior wall constituted a new subcolony (text-fig. 2B). The occurrence of numerous zooecial buds and the thickened zooecial walls within the new subcolonies suggest that this stage of growth was one of rejuvenation. However, intrazooecial fission of the type documented at a comparable position in other stenolaemates (Hillmer, Gautier and McKinney 1975) is not evident in *Blumenbachium*.

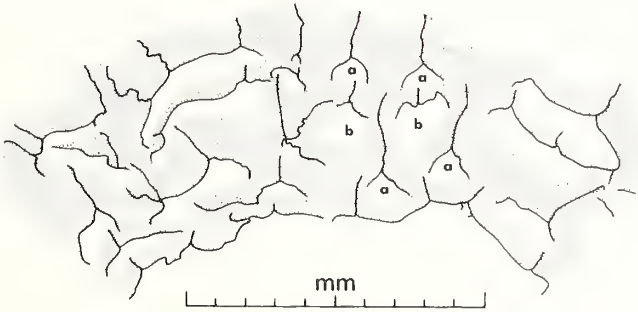
Each new subcolony apparently originated within the boundary walls of an established subcolony but in a variety of possible situations including ridge crests, ridge flanks, and depressions at the centres of the subcolonies. Commonly, two closely adjacent new subcolonies situated on either side of a ridge crest coalesced at an early stage in their growth, as in the model colony (text-fig. 4C). New subcolonies attained a low cup-shape by upward and outward growth. Continued growth caused them to overarch subcolonies of the previous generation and eventually to contact adjacent subcolonies. Instead of coalescing on contact, however, the bounding exterior walls of the subcolonies were retained and became interdigitated in the manner described previously (text-fig. 4D). A growth stage equivalent to the first growth stage (text-fig. 4A) had now been reached. Large colonies were constructed by several repetitions of this growth cycle.

The model colony (text-fig. 4) differs from a natural colony in the regularity of its subcolonies. Although subcolonies in fossil *Blumenbachium* are on average six-sided, some subcolonies may have only three sides and others may have eight or more sides. This variability (text-fig. 7) is largely a consequence of irregularity in the location of new subcolonies. Subcolonies are not evenly spaced. An additional geometrical factor precludes the possibility of a spheroidal colony being composed of hexagonal subcolonies. Space cannot be enclosed solely by hexagons (Thompson 1961, p. 157).

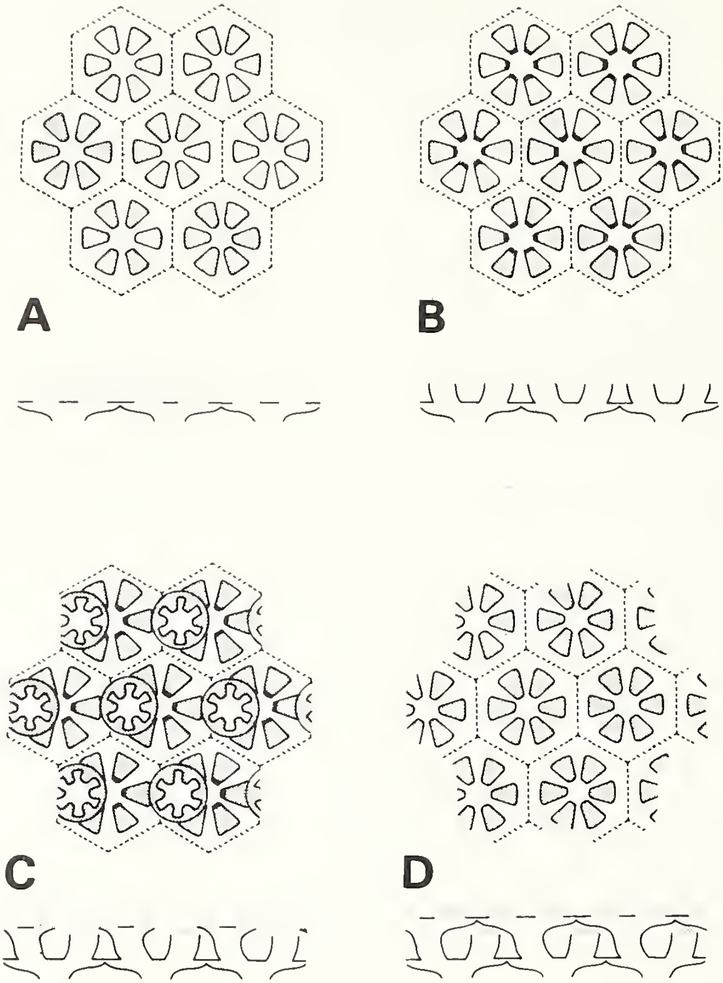


TEXT-FIG. 7. Subcolony shape drawn from the surface of a typical colony of *Blumenbachium globosum* Koenig (cf. text-fig. 4A). Boundaries between subcolonies are shown as solid lines and ridge sides as dotted lines. D 51069, Coralline Crag, Sudbourne, ×4.

Growth in *Blumenbachium* produced a multilayered colony (Pl. 55, fig. 6; Pl. 56, fig. 1) with each concentric layer consisting of a single generation of subcolonies united at their edges. Between the layers is enclosed a considerable volume of void space. Some of the colonies which have been sectioned reveal a variably defined dimorphism in the structure of the concentric layers with alternate layers being composed of relatively low-ridged and high-ridged subcolonies (text-fig. 8).



TEXT-FIG. 8. *Blumenbachium globosum* Koenig, D 6905. Drawing of part of a thin section through a colony showing three or four concentric growth cycles (cf. text-fig. 4D). Dimorphism in the growth cycles is well developed right of centre where two alternating types of lacunae are visible: a, lacunae between low subcolonies; b, lacunae between high ridged subcolonies.



TEXT-FIG. 9. Four stage (A–D) model of colony growth pattern in *Multifascigera debenensis* sp. nov. The top diagram for each growth stage is the surface of the colony, the bottom diagram is a vertical section. Exterior walls (enclosing fascicles and subcolonies) are shown by solid black lines, inferred hypostegal coelom is stippled, anastomoses between subcolonies are dashed, and the steep proximal sides of divergent fascicles are hatched. Full explanation in the text.

Multifascigera debenensis

None of the available colonies preserve early growth stages but comparison with known tubuloporinids of similar form (e.g. *Theonoa*) suggest that *Multifascigera debenensis* colonies may have begun growth as adnate fan-shaped expansions which later became discoidal when lateral lobes of the fan coalesced behind the ancestrula (see Borg 1926). The apertures of zooecia in early parts of colonies may have been isolated from one another, as in *Theonoa*, with later zooecial apertures grouped into fascicles.

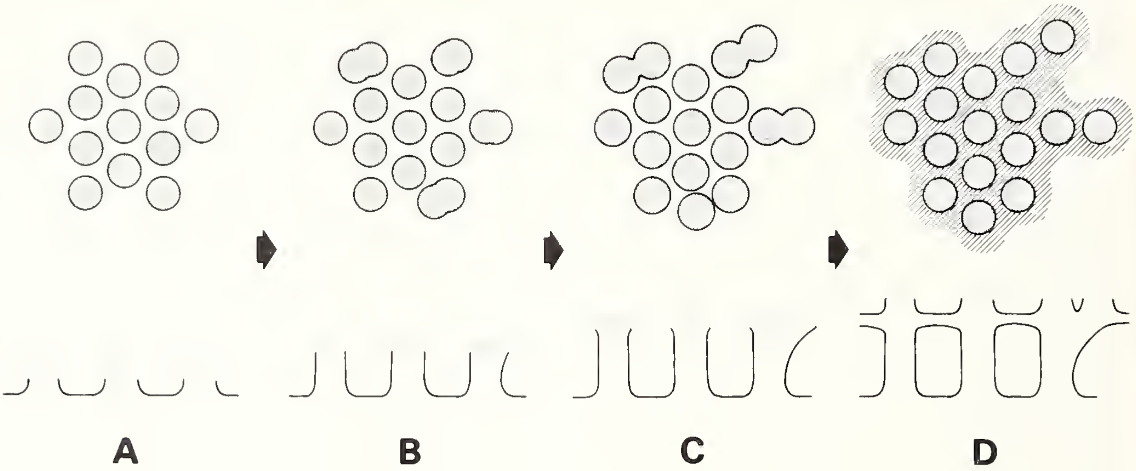
Surfaces of large colonies show numerous subhexagonal subcolonies each having a series of radially arranged fascicles (text-fig. 9A). These fascicles are typically four-sided, broaden towards the outer edge of the subcolony, and are surrounded by pseudoporous exterior wall which covers the upper surface of the subcolony between fascicles. Boundaries between adjacent subcolonies are indistinct (dotted in text-fig. 9) and sections show that subcolonies are not separated from one another by exterior walls as in *Blumenbachium*. Interzooecial walls (interior walls) bordering contiguous zooecial apertures are exposed on the upper surfaces of the fascicles. This implies the presence of hypostegal coelom capping each fascicle during colony life. Fascicles were initially extended obliquely upwards by the lengthening of existing zooecia (text-fig. 9B). A minority of fascicles, about one per subcolony, then grew rapidly upwards and outwards to overarch the other fascicles (text-fig. 9C). Each of these fascicles was destined to become a new subcolony within a new generation of subcolonies. Exterior wall was formed over the centre of the upper surface of the incipient subcolonies and in a series of strips radiating outwards from this central area. This exterior wall resulted from the division of interzooecial walls on meeting the outer epithelium covering the hypostegal coelom (see Taylor 1978, text-fig. 8) which capped the original fascicle. The extent of hypostegal coelom was now restricted to a series of strips on the surface of the incipient subcolony. Continued lateral expansion of subcolonies occurred by the extension of existing zooecia and budding of new zooecia on the budding lamina formed by the exterior wall which bounded the original fascicle. Adjacent subcolonies eventually met and coalesced (text-fig. 9D) to form a complete platform or layer across the colony surface. Because the new subcolonies of the model colony are equidistantly spaced, each subcolony attains a hexagonal plan view. However, both the shape of the subcolonies and the number of fascicles per subcolony vary considerably in natural colonies (Pl. 54, fig. 1). Growth of exterior wall on the upper surface of each subcolony in the model colony results in the isolation of six fascicles per subcolony. The model (text-fig. 9D) has now reached a stage equivalent to the first growth stage (text-fig. 9A) although the new subcolonies are not aligned directly above the original subcolonies. Large multilayered colonies were constructed by numerous repetitions of this growth cycle.

Meandropora tubipora

As in the two previous cyclostome species, colonies of *Meandropora tubipora* are organized into a series of subcolonies. In *Meandropora* these are columnar fascicles (Pl. 55, fig. 2) consisting of elongate zooecia surrounded by a pseudoporous exterior wall. Zooecia open at the tops of the fascicles where the existence of exposed interzooecial walls (interior walls) indicates the presence of a capping hypostegal coelom during life. Each fascicle would have possessed a separate hypostegal coelom which was not confluent with those of other fascicles.

Thirteen fascicles are shown in the surface view of the model colony (text-fig. 10A). Three of the fascicles are cut medially in the section beneath. Upward fascicle growth (text-fig. 10B) was achieved principally by the lengthening of existing zooecia. Budding of new zooecia was subordinate and occurred either by interzooecial wall division within the fascicle or on the budding lamina formed by the exterior wall bounding the fascicle. Colony growth usually involved an increase in the surface area of the colony and necessitated intercalation of new fascicles, formed by fascicle division, if constant fascicle spacing was to be maintained. During their upward growth, fascicles first became elongated along the axis in which division was to occur (text-fig. 10B) and then constricted centrally until they divided into two (text-fig. 10C). The two new fascicles were each bounded by an exterior wall and each would have had its own capping of hypostegal coelom.

A characteristic feature of growth in *M. tubipora* was the regular anastomosis of fascicles. After an increment of upward growth, the fascicles began to expand laterally (text-fig. 10C), apparently by increased zooecial budding on the lamina formed by the fascicle-bounding exterior wall. Eventually adjacent fascicles met and coalesced. Their bounding exterior walls broke down on coalescence suggesting hypostegal coelomic continuity between fascicles and the existence of a single extensive hypostegal coelom over the surface of the colony. Fascicle coalescence gave an extensive platform of zooecia which is shown to be complete and continuous in the model (text-fig. 10D). In fossil colonies, however, gaps in the platform are common and are a consequence of the failure of certain expanding fascicles to reach adjacent fascicles (Pl. 54, fig. 3). After formation of the platform a new generation of fascicles arose on the surface of the colony (text-fig. 10D). These new fascicles are usually situated almost directly above fascicles of the previous generation. They were isolated from one another by the secretion of exterior walls, in the form of terminal diaphragms (Nye 1968), occluding the orifices of the short zooecia (?kenozooids) occupying the platform between fascicles (Pl. 54, fig. 3). Continued upward growth of the new fascicles resulted in a situation equivalent to that of the first growth stage (cf. text-figs. 10A and 10D). Large colonies were constructed by numerous repetitions of this cycle of growth. When these colonies are fractured open, the platforms formed by fascicle coalescence appear as prominent concentric bands (Pl. 55, fig. 2).



TEXT-FIG. 10. Four stage (A–D) model of colony growth pattern in *Meandropora tubipora* (Busk). The top diagram for each growth stage is the surface of the colony, the bottom diagram is a vertical section. Fascicle-bounding exterior walls as shown by solid black lines, inferred hypostegal coelom (covering the growing edges of fascicles) is stippled, and the platform extending between fascicles is hatched in surface view. Full explanation in the text.

Meandropora aurantium

The growth pattern of *M. aurantium* colonies is similar to that of *M. tubipora* colonies but colonies generally lack abrupt and regular fascicle anastomosis. Consequently, *M. aurantium* colonies do not possess the concentric platforms which characterize *M. tubipora*.

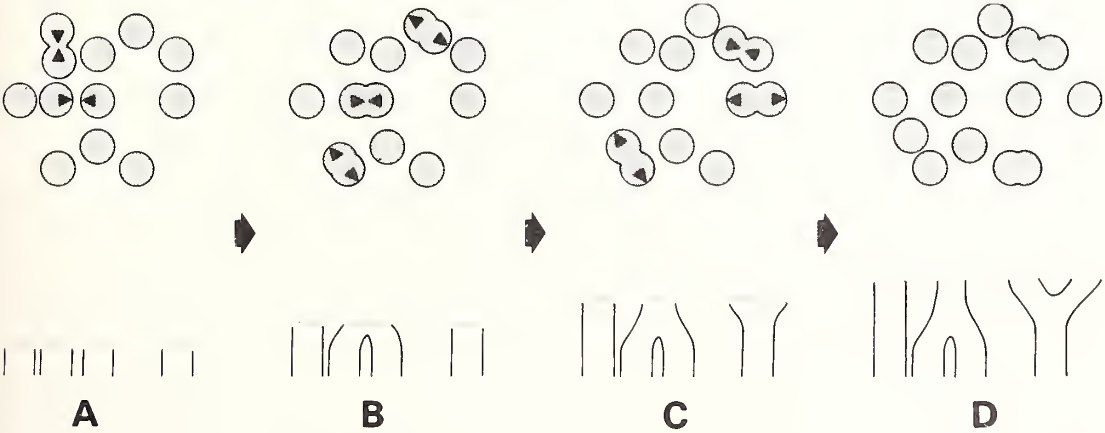
The columnar fascicles of *M. aurantium* are each bounded laterally by pseudoporous exterior wall and zooecia open at the tops of the fascicles where hypostegal coelom existed during life. Extension of fascicles was achieved largely by lengthening existing zooecia, although new zooecia were occasionally budded either by interzooecial wall division within fascicles or on the budding lamina formed by the fascicle-bounding exterior wall. Both division of established fascicles to form new fascicles and anastomosis of fascicles usually proceeded in an irregular manner during upward colony growth, as shown in the model colony (text-fig. 11). Fascicle division followed medial constriction of enlarged fascicles with elliptical cross-sectional shapes; fascicle anastomosis was brought about by the breakdown of exterior walls between converging fascicles. Some colonies (Pl. 56, figs. 6, 7) exhibit concentric bands (up to 1 cm deep) which were the result of periods of extensive fascicle anastomosis and minimization of interfascicular space (Pl. 54, fig. 5).

PALAEOECOLOGY

Coralline Crag facies and bryozoan distribution

The Coralline Crag was deposited during a Pliocene marine transgression over part of east Suffolk. The most conspicuous facies formed during this transgression is a sandwave facies deposited by an offshore sandwave field (facies B). The elongate nature of the outcrop of this facies may be evidence that the facies represents a Pliocene offshore linear sandbank comparable to those off Norfolk at the present time. To the west, on the inferred landward side of this sandwave field is a more silty sublittoral facies (facies A). In some places the sandwave facies is seen to overlie this more nearshore facies. To the north and east on the inferred seaward side of the sandwave facies is a facies of coarse skeletal carbonates (facies C). Nio (1976), in a discussion of the role of marine transgressions in the formation of sandwave complexes, described the sequence of facies which results from increasing water depth. Where water depth is sufficient, strong tidal currents offshore may result in the formation of large sandwaves (sandwave facies). Sandwaves will not develop in shallower sublittoral waters. In deeper offshore waters water depth may be too great and/or currents too weak for the production of large sandwaves. With increasing water depth during the transgression these facies migrate landwards with the more offshore facies overstepping the onshore facies. This facies sequence has been recognized in the Coralline Crag. Each facies has a characteristic lithology and fauna (Balson 1981) which are summarized below.

1. *Facies A*. Bioclastic silty sands were deposited on the landward side of the sandwave facies. This facies is best seen in the Ramsholt area where the sediments show evidence of intense bioturbation which has obliterated any previously existing sedimentary structures. The sediment is generally more poorly sorted and has a higher terrigenous content than that of the sandwave facies indicative of weaker currents and greater proximity to the shoreline. This facies usually contains a rich, diverse, and well-preserved fauna. Large infaunal bivalves (e.g. *Glycymeris*) are common and are frequently articulated indicating minimal reworking of the sediment by currents. Bryozoans are abundant including large irregular celleporiform (see Schopf 1969 for terminology and descriptions of bryozoan growth-forms) cheilostomes which formed substrates for organisms such as the coral *Cryptangia* (Buge 1952; Pouyet 1978). Erect eschariform and adeoniform colonies of *Metrarabdotos* are also common. These bioturbated sediments are overlain by coarser bioclastic sediments showing trough cross-stratification produced by megaripples with amplitudes of approximately 50 cm. The foresets frequently have silt drapes indicating periods of increased fine sediment input which may be related to storm events. Demonstrably *in situ* fauna is much rarer in this upper part of facies A.



TEXT-FIG. 11. Four stage (A–D) model of colony growth pattern in *Meandropora aurantium* (Milne Edwards in Lyell). The top diagram for each growth stage is the surface of the colony, the bottom diagram is a vertical section. Fascicle-bounding exterior walls are shown by solid black lines and inferred hypostegal coelom (covering the growing edges of fascicles) is stippled. Divergent arrowheads indicate dividing fascicles, convergent arrowheads anastomosing fascicles.

The environment of facies A was evidently one of sheltered inlets, formed by the drowning of a pre-existing topography. The large amount of fine sediment present may be due to a position at the end of a sediment transport path (Balson, in preparation). Deposition was relatively slow allowing extensive bioturbation. As water depth increased, tidal currents became established resulting in an increased coarse sediment input and the formation of megaripples.

Multifascigera debenensis is known exclusively from this facies where it occurs with occasional colonies of *Meandropora aurantium* and poorly preserved ?*M. tubipora*. *Blumenbachium globosum* is a notable absentee.

2. *Facies B*. The Coralline Crag of the Orford–Sudbourne area is characterized by the presence of large-scale cross-bedding produced by sandwaves of between approximately 1 and 3 m amplitude. The sandwaves were generated by dominantly unidirectional tidal currents flowing to the south-west. The fauna of this sandwave facies which is demonstrably indigenous is sparse and has a low diversity. Bivalve shells tend to be fragmented and abraded. Deposition was probably rapid but sporadic, resulting in well-defined individual foreset laminae. Periods of deposition were characterized by large amounts of bedload transport and reworking of bottom sediments, perhaps during storms. The bioclastic sand of the sandwave facies is consequently well-sorted with the carbonate material comminuted and highly abraded. Environments of this type are not easily colonized by benthos and it is likely that the abraded skeletal fragments, including those of *Meandropora* and *Blumenbachium*, were transported from elsewhere.

3. *Facies C*. This facies formed on the seaward side of the sandwave field and is now exposed in the Aldeburgh area as bioclastic sands with bedding horizontal or dipping at low angles. The sediment is generally coarse skeletal sand with only small quantities of fine or terrigenous sediment grains. The occurrence of occasional silt drapes indicates periodic increased deposition of fine sediment which may be related to storm events. The benthic fauna is both abundant and diverse. Moulds of large, often articulated, aragonitic bivalves may reveal clionid borings and encrustation by bryozoans. Calcitic bivalves such as *Chlamys* may also have an abundant and well-preserved encrusting epifauna which includes serpulids and bryozoans with membraniporiform and celleporiform growth-forms. Other celleporiform colonies are penetrated by narrow cylindrical voids which were probably left after the decomposition of an organic substrate, e.g. a hydroid. Horizontal burrows are locally abundant in this facies. The presence of articulated cellariiform bryozoan colonies is particularly notable. The calcareous internodes of these bryozoans were originally held together by chitinous nodes which would have decayed soon after death (Lagaaij and Gautier 1965). Preservation of articulated internodes implies minimal transportation and rapid burial. It appears that facies C was formed in an environment not influenced by strong currents (cf. sandwave facies) where bedload transportation was less prominent. Prevailing sedimentation rates may have been low, allowing the development of a diverse epifauna and extensive bioturbation between sporadic larger influxes of sediment.

The large cyclostomes reach their greatest abundance in facies C. *Blumenbachium* is particularly numerous and some colonies are penetrated by cylindrical voids in the same way as the celleporiform cheilostomes. Fine-grained sediment settling from suspension on to the surface of the large cyclostomes could be cleared by the powerful extrazooidal feeding currents (Taylor 1979) the bryozoans may have created during life.

Development of different colony shapes

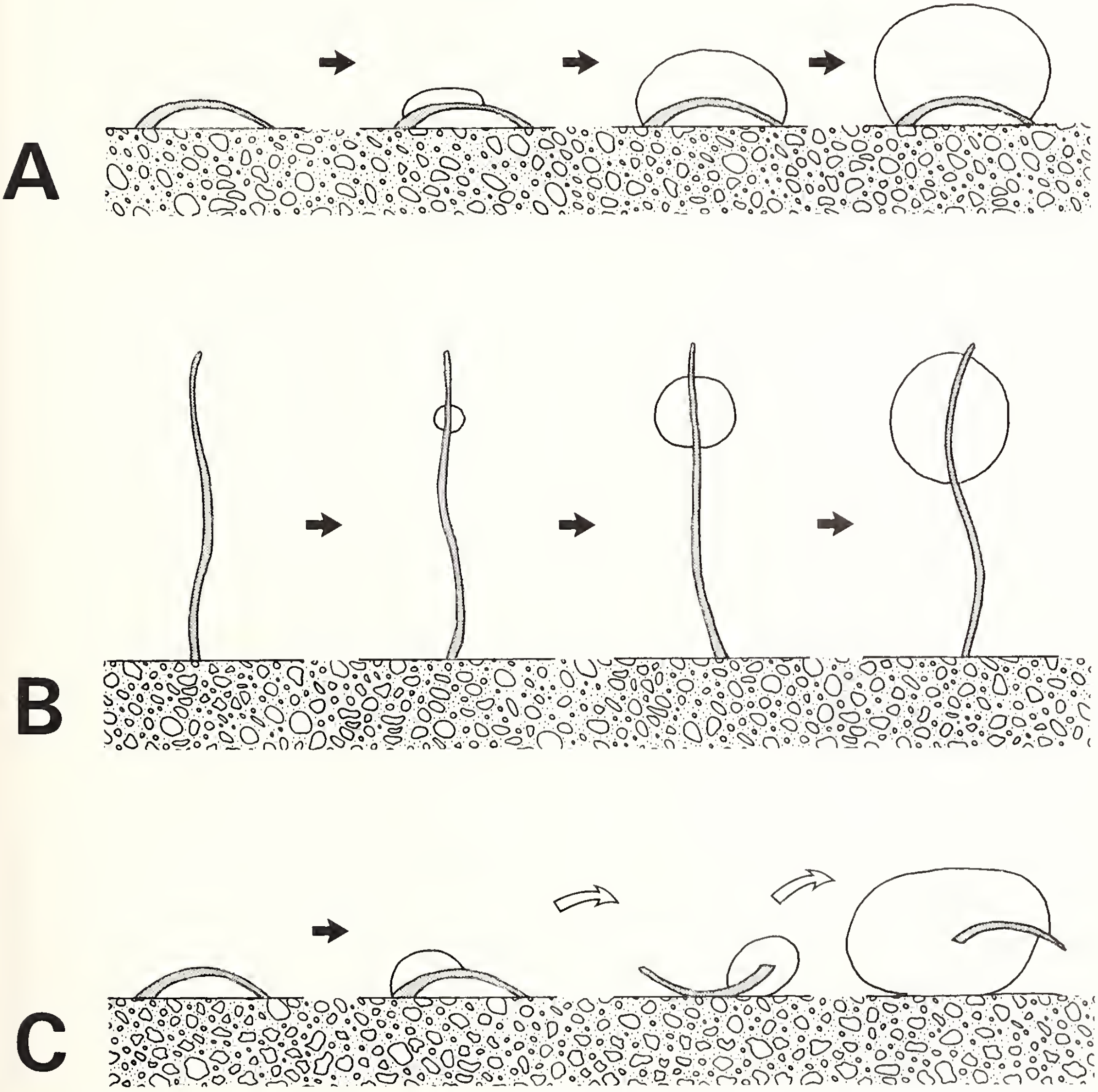
Three distinct colony types can be recognized among the large cyclostomes on the basis of inferred developmental history (text-fig. 12).

1. *Colonies which had an external basal substrate*. These colonies developed in the conventional manner for a sessile bryozoan (text-fig. 12A). The substrate they encrusted remained comparatively stable on the sediment surface and consequently had a permanent undersurface inaccessible to the bryozoan. Semi-erect bryozoan growth on the upper surface of the substrate gave a mound-like colony with a moderately high sphericity (Pl. 55, fig. 6; Pl. 56, fig. 6).

2. *Colonies which were supported by an unpreserved cylindrical substrate*. In these colonies the original substrate is represented by a narrow cylindrical void which was probably left after the decay of a perishable organic substrate such as a hydroid. This substrate evidently held the colony above the sea-bed (text-fig. 12B) enabling bryozoan growth to proceed equally in all directions and resulting in a colony with a very high sphericity (Pl. 56, fig. 2).

3. *Colonies which enveloped an originally external basal substrate*. Perhaps the most interesting colonies are those which partly (Pl. 56, fig. 7) or totally (Pl. 56, figs. 3, 4) envelope their original substrate of attachment. Their substrate was evidently a mobile skeletal fragment lying on the

sea-bed. Changes in the orientation of the substrate brought different portions of the bryozoan colony into contact with the sediment surface and while these parts undoubtedly ceased to grow, other parts of the colony continued to grow. An originally external basal substrate could only become totally enveloped (text-fig. 12C) by being overturned. Comparable colony forms have been previously described in fossil and living bryozoans (Flor 1972; Rider and Enrico 1979). Morphological and developmental comparisons can also be made with algal rhodoliths (Bosellini and Ginsburg 1971; Focke and Gebelein 1978) and certain colonial corals (Kissling 1973; Glynn 1974)



TEXT-FIG. 12. Development of different colony shapes in large cyclostomes from the Coralline Crag. A, four stages in the development of a colony attached to a substrate (stippled bivalve shell) resting stably on the sea-bed. B, colony supported above the sea-bed by an erect, soft-bodied substrate. C, circumrotatory colony partially enveloping a substrate (bivalve shell) which was overturned.

which have been termed 'circumrotatory'. This term is here applied in a developmental rather than strictly morphological sense to describe bryozoan colonies which were reorientated during their growth. Conversely, colonies which evidently maintained a constant orientation are referred to as non-circumrotatory. Application of a developmental distinction avoids confusion between circumrotatory colonies and non-circumrotatory colonies whose radial growth was the result of being supported above the sediment surface (colony type B above).

The nature of the substrate may have been a major factor determining whether colonies achieved circumrotatory growth. Bivalve shells appear to have been the commonest substrates colonized by the large cyclostomes. These shells would have formed comparatively stable substrates when orientated in a convex upwards attitude (e.g. Pl. 55, fig. 6). Indeed, many colonies attached to bivalve shell substrates are non-circumrotatory; those which are circumrotatory have a fairly low sphericity because the flat shape of the bivalve is strongly reflected in the shape of the bryozoan colony (e.g. Pl. 56, fig. 7). High sphericity as a result of circumrotatory growth is often seen when the substrate is small, e.g. bryozoan (Pl. 56, figs. 3, 4) and shell fragments. Small substrates were easily overturned and their shape was not strongly reflected in the shape of the bryozoan colony. Other substrates utilized commonly include turritellid gastropods (Pl. 56, fig. 5). Some colonies evidently gained secondary substrates, including fragments of other bryozoans, during their growth. These secondary substrates probably rested on the sea-bed adjacent to the growing bryozoan colony and became overgrown. Some were totally enveloped during subsequent bryozoan growth.

Overturning of circumrotatory colonies

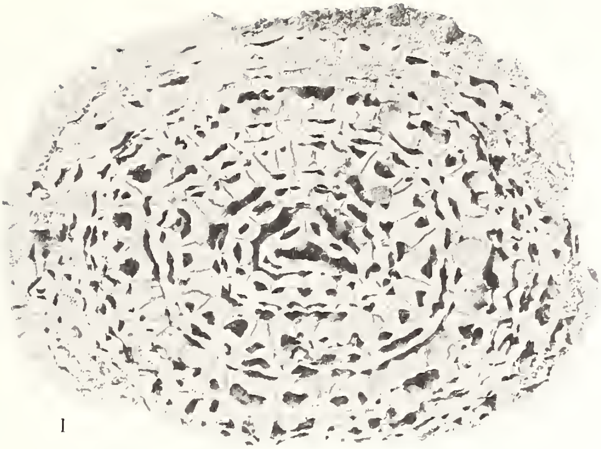
Circumrotatory growth necessitated overturning of the bryozoan colony and its substrate. This could have been achieved in two principal ways: by current action or by mobile benthic animals. Rider and Enrico (1979) and Kissling (1973) believed that currents were largely responsible for overturning the circumrotatory bryozoans and corals they studied whereas Glynn (1974) thought that overturning was accomplished by animals (e.g. fishes and crustaceans) in search of food and possibly shelter. If currents were responsible for overturning the Coralline Crag cyclostomes the attainment of circumrotatory growth should be more closely related to colony size, and thus stability, than is actually evident (but cf. Kobluk, Bottjer and Risk 1977). No examples have been found where an initially circumrotatory colony later became non-circumrotatory as enlargement increased stability. The Coralline Crag cyclostomes also lack the symmetry of internal structure and sphericity of external form which characterizes probable current-overturned circumrotatory bryozoans (e.g. Pedley, in preparation). The apparent restriction of the large cyclostomes to facies A and C where bedload transportation is least evident, further suggests biological overturning. This may have been accomplished by crabs and fishes which are known to have lived sympatrically with the bryozoans (Bell 1897) or by infauna burrowing in the sediment beneath the bryozoan colonies (the biological bulldozers of Thayer 1979).

EXPLANATION OF PLATE 56

Figs. 1, 3–4. *Blumenbachium globosum* Koenig. 1, ellipsoidal colony (probably circumrotatory) with origin close to centre, D 52755, lectotype, 'White Crag', Suffolk, × 1·1. 3–4, part and counterpart of circumrotatory colony totally enveloping a celleporid cheilostome, D 51070, Coralline Crag, Suffolk, × 1·2.

Figs. 2, 6–7. *Meandropora aurantium* (Milne Edwards in Lyell), Coralline Crag. 2, spheroidal colony penetrated by a narrow cylindrical cavity (not visible in photograph) evidently left after decomposition of a substrate which supported the colony above the sea-bed (cf. text-fig. 12B), Sedgwick Museum C 51085, Sudbourne Hall, × 0·75. 6, hemispherical colony (cf. text-fig. 12A) with growth banding, D 52775, Aldeburgh Hall, × 1·1. 7, circumrotatory colony partly enveloping a bivalve shell represented by a curved hollow (cf. text-fig. 12C), D 52766, Aldeburgh Hall, × 1·05.

Fig. 5. *Meandropora tubipora* (Busk), colony attached to a turritellid gastropod, Coralline Crag, Sudbourne, × 0·9.



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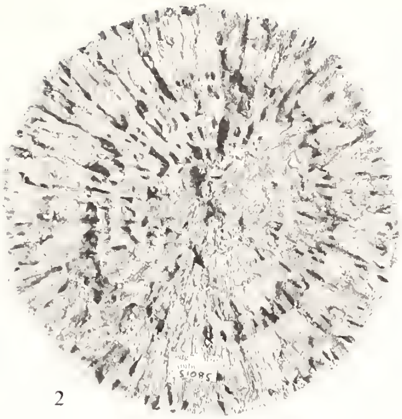

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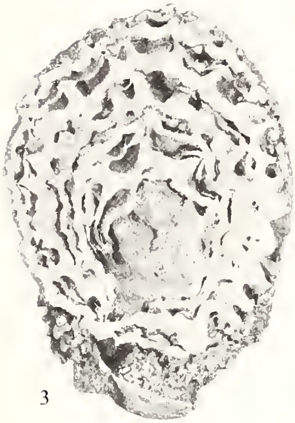

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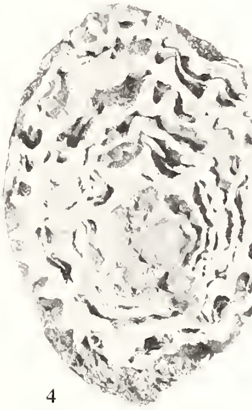

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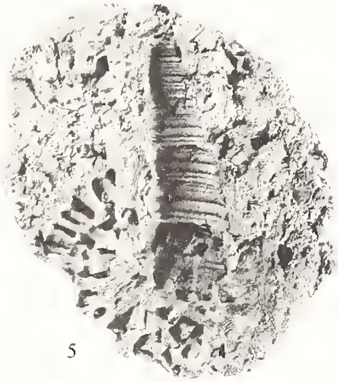

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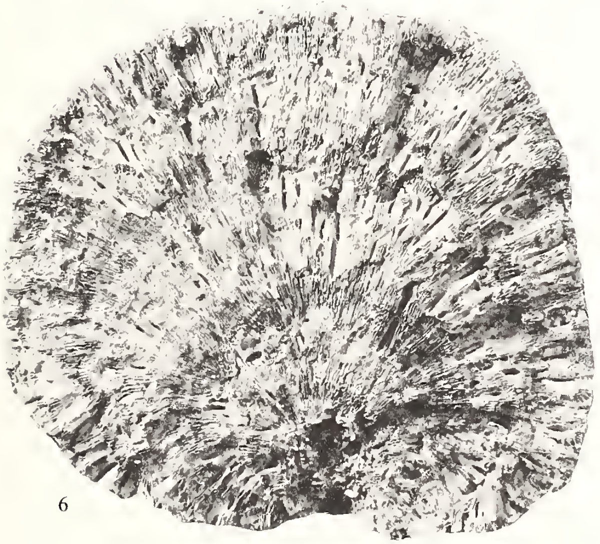

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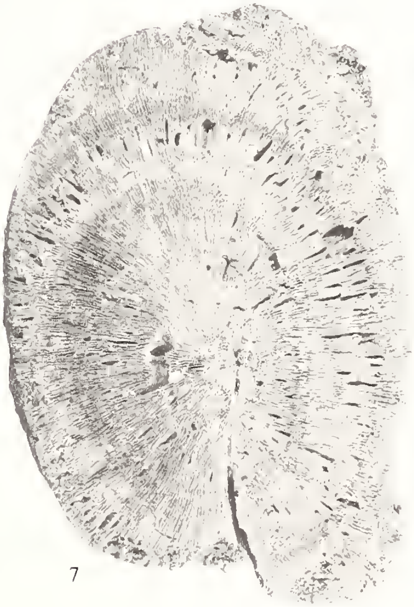

7

BALSON and TAYLOR, Pliocene bryozoans

Biotic associates

A conspicuous feature of several colonies is the presence of a large cavity (cf. Glynn 1974) where the earliest-formed parts of the colony and its substrate have been removed (Pl. 55, fig. 1). These cavities truncate skeletal walls and may have a narrow entrance which broadens into a large chamber. Comparable cavities have been described from the Recent by Warme and McHuron (1978) and are also present in living celleporid bryozoans from the Scilly Isles which are the domiciles of crabs (P. J. Hayward, pers. comm. 1978). The Coralline Crag examples may have resulted from the activity of microborers (e.g. algae) and macroborers (e.g. polychaetes) forming an initial cavity and weakened area which could be enlarged by a crab, possibly while the bryozoan was still living. It may be significant that other objects large enough to provide shelters for crabs etc., are rarely preserved in Coralline Crag sediments.

The Coralline Crag cyclostomes often acted as substrates of attachment for various encrusting animals including membraniporiform cheilostomes and serpulid worms (Pl. 55, fig. 5). In several cases the host cyclostome subsequently overgrew these encrusters, thus proving their life association. Serpulids, for example, are often found partly or wholly immersed within colonies of *Blumenbachium globosum*. They evidently colonized the surface of the bryozoan but were covered when a new generation of overarching subcolonies formed. It seems possible that much of this encrusting epifauna became established during periods (?seasonal) of colony dormancy.

DISCUSSION

Subcolonial organization

The four large cyclostomes from the Coralline Crag exhibit a feature commonly found in post-Palaeozoic cyclostomes: division of the colony into a series of subcolonies or cormidia each bounded laterally and/or basally by a calcified exterior wall. This has been described previously in a variety of multilamellar cerioporinids, e.g. Lower Cretaceous *Multicrescis* and *Reptomulticava* (Flor and Hillmer 1970; Hillmer 1971; Hillmer, Gautier and McKinney 1975; Maryanska 1968; Nye and Lemone 1978). It is also known in several tubuloporinids, including fasciculate forms (e.g. *Fasciculipora*, see Malecki 1980) and non-fasciculate forms (e.g. *Cellulipora*, see Buge and Voigt 1972), in melicerititids (*Reptomultelea*), and in rectangulates (e.g. *Lichenopora* spp., see Chapman 1933; Buge 1975). Most of the zooids comprising the cormidia in each of these cyclostomes are skeletally similar and undoubtedly functioned as feeding zooids (autozooids), although some or all cormidia within a colony may also contain non-feeding polymorphs (kenozooids, gonozooids, and, in *Reptomultelea*, mandibulate zooids). In general, cyclostome cormidia appear not to be functional units of the colony in the sense of cheilostome cormidia (Ryland 1979) where the cormidium consists of a group of different polymorphs each performing a different function. Instead, cyclostome cormidia seem to serve as structural units ('building blocks') and probably also as physiological units of the colony.

Cormidia in related bryozoans of the Palaeozoic order Trepostomata have been recently analysed by Anstey and co-workers (Anstey and Delmet 1973; Anstey, Pachut and Prezbindowski 1976; Pachut and Anstey 1979; Podell and Anstey 1979). Trepostome cormidia are centred around protuberances on the colony surface known as monticules. Apart from having a role in filter-feeding (Banta, McKinney and Zimmer 1974; Taylor 1979), monticular cormidia were probably physiological units of the colony. Zooidal budding and other physiological activities seem to have been controlled by morphogens released by zooids at the centre of each monticule. One of the major differences between these monticular cormidia and the cormidia of post-Palaeozoic cyclostomes is that trepostome cormidia do not have well-defined boundaries because they lack the exterior walls which border cyclostome cormidia. The greater skeletal autonomy evident in cyclostome cormidia reflects a greater autonomy of soft parts. Surfaces of trepostome colonies during life were apparently enclosed beneath a common or hypostegal coelom which was colony-wide and continuous across cormidial boundaries (Boardman 1971). However, the presence of calcified exterior walls at the boundaries of cyclostome cormidia implies that hypostegal coelom did not extend between cormidia; the distal growing edge of the exterior wall marks the limit of hypostegal coelom (e.g. Boardman 1971, fig. 2). Each cyclostome cormidium possessed a separate hypostegal coelom. In the absence of a colony-wide hypostegal coelom, soft tissue connection between cyclostome cormidia could be achieved only via the interzooidal pores (Nielsen and Pedersen 1979) which penetrate interior walls between zooids. These pores probably allowed activities of individual cormidia (e.g. growth) to be co-ordinated in cyclostomes whereas the colony-wide hypostegal coelom and associated membranes may have the necessary intercormidial connections in trepostomes which lack interzooidal pores. Interzooidal pores are infrequently developed in Palaeozoic stenolaemates (cf. ceramoporoid cystoporates and some cyclostomes, see Utgaard 1973, Brood 1975) and their proliferation during the post-Palaeozoic may have paved the way for the evolution of diverse stenolaemates with well-defined cormidia bordered by calcified exterior walls.

The widespread occurrence of exterior wall bounded cormidia in post-Palaeozoic cyclostomes belonging to diverse taxa implies that this type of organization confers adaptive advantages. Subdivision of colonies resulting in decentralization may allow more precise control of zooid activities and responsiveness to environmental heterogeneities both within and between colonies. A further significant advantage may relate to the localization of colony damage. In a large colony with an extensive colony-wide hypostegal coelom, coelomic rupturing may have a widespread effect, disrupting both feeding and growth until repair could be completed. In a large colony with many small cormidial hypostegal coeloms, coelomic rupturing may be localized to a single coelom leaving most of the colony unaffected. This would have been particularly important to those Coralline Crag cyclostomes which seem to have been regularly overturned.

The large cyclostomes of the Coralline Crag evidently lived attached to a wide variety of substrates. While some colonies were supported above the sea-bed by soft-bodied organisms others utilized shells, varying in shape, size, and stability, resting on the sea-bed. This indicates a relative lack of habitat selection by the settling bryozoan larvae and would have meant that developing colonies may have encountered a variety of different small-scale environmental conditions. Like many plants (Bradshaw 1965), colonial animals can respond to habitat variations by phenotypic plasticity in growth. The large cyclostomes from the Coralline Crag had the capacity to mediate a plastic response not only at zooidal level but also at the additional hierarchical level of the subcolony.

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LATE JURASSIC INOCERAMID BIVALVES FROM THE ANTARCTIC PENINSULA AND THEIR STRATIGRAPHIC USE

by J. A. CRAME

ABSTRACT. The majority of inoceramid bivalves occurring in Late Jurassic temperate realm assemblages can probably be assigned to the genus *Retroceramus*. Although there are a few transitional forms, *Retroceramus* can generally be distinguished from the better-known genus *Inoceramus* by features of both the external and internal shell morphology. The replacement of *Retroceramus* by *Inoceramus* in the Early Cretaceous may reflect the adoption of an epibyssate mode of life, and probably represents one of a series of endo- to epibyssate life habit transitions that occurred during the evolutionary history of the Inoceramidae.

Four common Late Jurassic species of *Retroceramus* form the basis of an inoceramid zonation that can be used for local correlations within western Antarctica, and regional correlations throughout the Southern Hemisphere. Isolated exposures in the Antarctic Peninsula can be correlated with the Fossil Bluff Formation (Kimmeridgian–Albian) of eastern Alexander Island, and it should eventually be possible to correlate the latter unit with the extensive Jurassic Latady Formation (?Bajocian–Tithonian) of the Lassiter and Orville coasts. Used in conjunction with existing cephalopod biozones, this zonation scheme indicates that the lower levels of the Fossil Bluff Formation correlate with the Lower, Middle, and Upper Spiti Shales of the Himalayas and both the Ohauan and Puaroan stages of the New Zealand Jurassic. Tentative correlations can also be made with areas such as South America, New Caledonia, Indonesia, and Western Australia.

The occurrence of genera such as *Retroceramus*, *Anopaea*, and *Buchia* in western Antarctica does not necessarily indicate the existence of a late Jurassic anti-Boreal faunal realm. Available evidence suggests that the distribution of benthic faunas at this time was probably controlled by a series of distinctive sedimentary facies which extended around much of the southern margins of Gondwana, rather than by pronounced climatic zonation.

THE value of inoceramid bivalves in Cretaceous biostratigraphy has now been firmly established. They have been used extensively to erect local zonations in both the Northern and Southern Hemispheres, and there is a considerable volume of evidence to show that they may also be of prime importance in regional biostratigraphical correlations (e.g. Kauffman 1966, 1977*a*; Pergament 1978; Crame 1981*a*). Inoceramids appear to have been ecologically tolerant bivalves, able to live at various depths and on diverse substrates. They are one of the commonest elements in both temperate and tropical Cretaceous macro-benthic assemblages and are of particular importance in dating and correlating those sedimentary sequences that lack either ammonites or planktonic microfossils. Kauffman (1968, 1970, 1975, 1977*b*, 1978) has shown that, in addition to their wide facies tolerance, inoceramids had a potential mechanism for rapid, widespread dispersal (probably by means of a planktonic larval stage), and very fast evolutionary rates. In the Upper Cretaceous they may well offer a stratigraphical framework for regional correlations superior to that already provided by the ammonites (Kauffman 1975, p. 170).

Jurassic inoceramids, on the other hand, have been much less widely used in biostratigraphy, especially by European and North American geologists. This is no doubt partly a consequence of the existence of a ready alternative group of zone fossils in the ammonites, and partly a consequence of the comparative rarity of inoceramids in the European reference sections. However, viewed on a global scale, Jurassic inoceramids are a widespread group, dominating many macro-benthic assemblages in both the North and South Temperate faunal realms. They are known to be particularly abundant in the Siberia–Alaska region, Japan, and around the southern margins of

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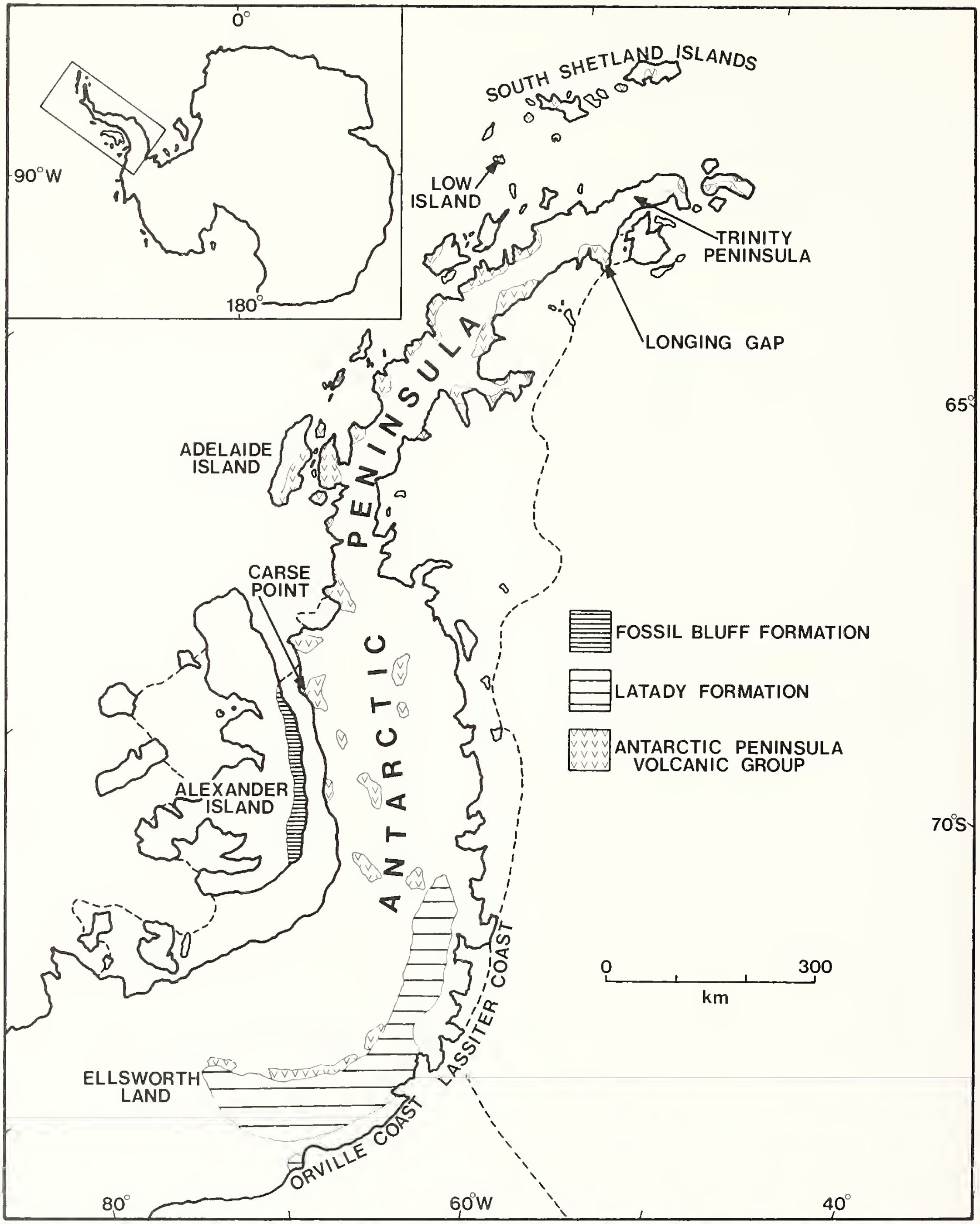


TEXT-FIG. 1. Sketch-geological and locality map of the Antarctic Peninsula. The map shows the principal outcrops of the three sedimentary formations from which Late Jurassic fossils have been obtained. The dashed lines indicate the approximate limits of ice shelves. (N.B. British geologists normally refer to the Lyon Nunataks-Behrendt Mountains region rather than Ellsworth Land.)

the ancient Gondwana supercontinent. Local zonations based on Jurassic inoceramids have been established for Siberia (e.g. Koshelkina 1957, 1959, 1960, 1963; Zakharov and Shurygin 1978), Japan (Hayami 1960, 1961), Himalayas (Spiti) (Stevens 1965), Indonesia (Stevens 1965; Westermann, Sato and Skwarko 1978), New Zealand (Fleming and Kear 1960; Speden 1970; Stevens and Speden 1978), and western Antarctica (Thomson and Willey 1972; Quilty 1977; Taylor, Thomson and Willey 1979). Both Hayami (1960, p. 227) and Koshelkina (1963, p. 136) have emphasized their potential in regional correlations, and Stevens (1965) has used them to help correlate Late Jurassic successions of the Himalayas (Spiti) with those of Indonesia and New Zealand.

It is the intention of this work to show the importance of Jurassic inoceramids in both local and regional biostratigraphy by concentrating on a group of Late Jurassic species from the Antarctic Peninsula (which for the purposes of this study is defined as the region in text-fig. 1 having its southern boundary at approximately latitude 72°S). These specimens were collected from a series of thick clastic and volcanogenic sedimentary rocks which accumulated in basins adjacent to an extensive island arc (e.g. Taylor *et al.* 1979; Thomson, in press). Similar sedimentary rocks of Middle to Late Jurassic age (the Latady Formation) are also known from the Lassiter and Orville coasts (Williams, Schmidt, Plummer and Brown 1972; Rowley 1978; Rowley and Williams, in press; Thomson, Laudon and Boyles 1978) and eastern Ellsworth Land (Laudon, Lackey, Quilty and Otway 1969; Laudon 1972) (text-fig. 1), and these too have yielded invertebrate assemblages rich in inoceramids. In time, it should be possible to establish a detailed succession of Middle to Late Jurassic inoceramid species for western Antarctica which will serve as a valuable reference section for the correlation of Southern Hemisphere Jurassic strata.

Southern Hemisphere Mesozoic rocks have in general received far less attention from biostratigraphers than their Northern Hemisphere counterparts, and there are still many gaps in our knowledge of both the nature and distribution of key index fossils. This is particularly so with the inoceramids, where considerable taxonomic and stratigraphical problems remain to be solved. Species concepts for Mesozoic bivalves are notoriously inconsistent, and those applied to Jurassic inoceramids are certainly no exception. Although most modern workers now base their species on the expected morphological variation within a fossil population (e.g. Hallam 1976, p. 246; Raup and Stanley 1978, p. 113), it is only too apparent that in the past a number of authors have applied a rigid species concept to the study of Southern Hemisphere inoceramids and identified new species on the basis of very limited material. Further problems are encountered when superspecific classifications are attempted. Heinz's (1932) famous paper on the classification of the Cretaceous Inoceramidae, containing no less than thirty-eight new genera, has now been dismissed by most workers as a classic example of 'over-splitting' (e.g. Sornay 1966, p. 26), and, perhaps in reaction to it, nearly all subsequent inoceramid classifications have been extremely conservative in their allocation of genera and subgenera. Indeed, the vast majority of described species have been assigned to a single genus, *Inoceramus*. By way of a contrast, Kauffman (1968) has argued strongly for a broader generic concept within the Inoceramidae, suggesting that features of the internal shell morphology, such as the hinge line, ligament pits, and muscle scars, could be used as additional taxonomic criteria. The very large number of apparently valid species and broad morphological variation shown by the group as a whole tend to support Kauffman's arguments, but, as will become apparent from the discussion below, there are considerable problems in assigning Jurassic species to meaningful generic groups.

Finally, it should be emphasized that the stratigraphical problems encountered in erecting detailed inoceramid biozones will be fully resolved only when many more specimens have been collected from accurately measured sections. As well as facilitating better correlations, precisely localized specimens will also greatly enhance the quality of current evolutionary and palaeobiogeographical studies.

A GENERIC CONCEPT FOR LATE JURASSIC INOCERAMIDS

It has not been generally appreciated that a variety of generic and subgeneric names are available for Jurassic inoceramids: Cox (1969) listed eight genera and six subgenera that are currently valid. That alternative names to *Inoceramus* are not more commonly used is probably a reflection of the considerable degree of confusion that exists today in Jurassic inoceramid taxonomy. It is hard to establish clear-cut working definitions for a number of genera and subgenera, and it is readily apparent that many of the available names have been inconsistently applied since their inception. Establishment of a viable generic concept must remain a major goal of Jurassic inoceramid palaeontology.

One of the first attempts to classify Jurassic inoceramids was that made by Rollier (1914), who thought that the majority of species could probably be referred to the subgenus *Inoceramus* (*Mytiloides*) Brongniart 1822. This was a rather bold and imaginative step to take, for hitherto *Mytiloides* had been regarded as an essentially Cretaceous subgenus, erected primarily to accommodate the distinctive Turonian species, *I. labiatus* (Schlotheim). At first sight, a number of Jurassic species do indeed seem to show the characteristics of this subgenus: the Liassic species, *I. falgeri* Ooster and some forms of *I. fuscus* Quenstedt (Aalenian–Bajocian), for example, have obliquely elongated outlines, fine concentric ornament, and short, oblique postero-dorsal wings. However, it is obvious that many Jurassic species do not possess either the typical outline or ornament pattern of this subgenus, and many of the more obliquely elongated types, such as *I. falgeri*, are still poorly known. At least some of the forms currently ascribed to *I. fuscus* may belong to *Retroceramus* (for a definition of this genus, see below), and it is apparent that until more precise information about the morphology of these Jurassic *Mytiloides*-like forms is available, it will not be possible to make anything other than tentative assignations to this subgenus. In particular, it will be argued below that detailed information on the structure of the hinge region and ligament pits is of crucial importance in generic diagnosis.

Cox (1969), Hayami (1975), and Quilty (1977) have all assigned the common Southern Hemisphere species, *I. galoi* Boehm, to the subgenus *Mytiloides*, but it will be suggested below that this species more likely belongs to the genus *Retroceramus* Koshelkina 1963. Hayami (1975, p. 51) also classified five other Japanese Jurassic species within *Mytiloides*: these are all small, rounded forms with faint to moderately developed concentric ornament (see Hayami 1960, pl. 15, figs. 11–16). *Inoceramus morii* Hayami (1960, pl. 15, figs. 11 and 12) appears to correspond well with the accepted *Mytiloides* morphology, but all the other species are of less certain affinity. Both *I. hashiurensis* Hayami and *I. hamadae* Hayami have erect outlines and appear to be prosogyrous, whilst *I.* (*Mytiloides*) sp. and *I.* aff. *fuscus* are known only from poorly preserved internal and external moulds, respectively. *Inoceramus* sp. aff. *I. galoi* (Hayami 1960, pl. 16, fig. 6) may well be a *Retroceramus*, belonging to the *R. morosus* Koshelkina group (Koshelkina 1969*b*, p. 76). Rollier (1914) established a second subgenus, *Mytiloceramus*, to contain certain Jurassic species which were obviously not obliquely elongated. The type of the subgenus, *I.* (*M.*) *polyplocus* Roemer, is medium-sized, has a distinctive rounded-rectangular outline, and is moderately inflated: there is no clearly delimited postero-dorsal wing. A noticeable additional feature of *I. polyplocus* is a byssal notch on the anterior margin, immediately beneath the umbo (e.g. Cox 1969, fig. C 47, 3). Hayami (1960, p. 299, pl. 15, fig. 7; 1975, p. 50) believed the Japanese species *I. karakuwensis* Hayami to be a *Mytiloceramus*, but Koshelkina (1969*b*, p. 60) reinterpreted it as a *Retroceramus*.

The first attempt at a comprehensive classification of Jurassic inoceramids was that made by Hayami (1960), who established four hypothetical stages in the development of the Inoceramidae. The first stage is marked by the development of the genus *Parainoceramus*, and is based on a morphologically cohesive group of small, simple forms restricted to the Upper Triassic–Middle Jurassic. The second, or differentiation, stage marks an explosive development of inoceramids at the Lower–Middle Jurassic boundary. Two groups (the *polyplocus* and *fuscus* groups) can be distinguished early in the stage, and later on three more appear (the *lucifer*, *retrorsus*, and *galoi* groups). The third, or *neocomiensis*, stage is marked by the appearance of strongly inequivalve species in the Upper Jurassic–Lower Cretaceous. Inoceramids were held to be rare in this stage, but diversified again in the fourth stage, which covers the rest of the Cretaceous.

The *Parainoceramus* group can be maintained as a distinct genus (Cox 1969, p. N320; Duff 1978, p. 48) and, as already discussed, the *polyplocus* group can be contained within the subgenus (or possibly genus) *Mytiloceramus*. The *fuscus* group, on the other hand, is less easily classified. Hayami (1960) established this group for subrhomboidal to obliquely elongated species in which wings are undeveloped, the postero-dorsal area ill-defined, and the concentric ornament irregularly and weakly developed. He obviously envisaged it to be the main trunk of the Inoceramidae through the Middle and Upper Jurassic (Hayami 1960, fig. 1). Of the twenty or so species ascribed to it, some show strong *Retroceramus* affinities and others may belong within *Mytiloides* (Hayami 1975): among the residue are a number of poorly known European species. It would seem, then, that in all probability this is a hybrid group, containing the representatives of at least two, and probably three, genera. The three groups appearing later in the second stage (the *lucifer*, *retrorsus*, and *galoi* groups) have mytiliform to subrhomboidal outlines, strong concentric ornament, and usually possess a well-defined postero-dorsal wing: as such, they all show strong affinities to *Retroceramus* Koshelkina (see below). Whereas the *Parainoceramus* group is cosmopolitan, the *fuscus* group is essentially European in its distribution. The *lucifer* and *retrorsus* groups arose in the Northern Hemisphere Boreal realm, and the *galoi* group in the so-called anti-Boreal realm of the Southern Hemisphere. The *neocomiensis* group is poorly represented in the Jurassic, for only one strongly inequivalve species, *I. maedae* Hayami (?Callovian), has so far been described.

Until now, the validity of assigning the vast majority of Jurassic inoceramids to the genus *Inoceramus* has not been seriously questioned. Most Jurassic species had, after all, shell forms and ornament patterns similar to the well-known Cretaceous species, and it was logical to assume that they should be allocated to the same genus. Those subdivisions that were suggested (by Rollier (1914) and Hayami (1960)) related primarily to the establishment of subgenera within the genus *Inoceramus*. The first indications that many (perhaps all) Jurassic species might in fact belong to a genus other than *Inoceramus* were given by Koshelkina (1963), who based his remarks on a detailed examination of the prodigious Siberian Jurassic inoceramid faunas. Koshelkina (1963, p. 135) suggested that the following general differences could be established between Jurassic inoceramid species and their Cretaceous counterparts:

(i) All Jurassic species were equivalve, but many Cretaceous species clearly were not.
(ii) The ligament area of Jurassic species was of quite different structure, being characterized by large irregular ligament pits that often fall into two distinct size classes. In Cretaceous inoceramids the ligament pits are typically narrow, elongated, and of uniform size.
(iii) Many Jurassic species have non-terminal beaks.

Koshelkina (1957, p. 29) initially distinguished three groups of *Inoceramus* (the *retrorsus*, *formosulus*, and *vachrameevi* groups), which he used as the basis of the subgenera *Retroceramus*, *Fractoceramus*, and *Costoceramus*, respectively. However, these names were not validated until 1959, when type species were designated and the name *Striatoceramus* substituted for *Costoceramus* (Koshelkina 1959, p. 100). *Retroceramus*, the largest subgenus, is characterized by subrhomboidal to obliquely oval valve outlines and regular, concentric ornament, *Fractoceramus* has a mytiliform outline and irregular ornament, and *Striatoceramus* a triangular outline and distinctive combination of radial and concentric ribs. As it became apparent that the majority of species fell within *Retroceramus*, Koshelkina (1963) subsequently elevated this subgenus to generic status; *Retroceramus*, *Fractoceramus*, and *Striatoceramus* were retained as subgeneric divisions of the new genus. In the same paper, Koshelkina (1963) also proposed that four other genera of Jurassic inoceramids could be distinguished. *Arcticeramus*, based on *I. arcticus* Koshelkina, was established as a new genus to accommodate two markedly inequivalve Upper Jurassic species, and is equivalent in concept to Hayami's (1960) *neocomiensis* group. *Anopaea* Eichwald was retained as a distinct genus as it has such an unusual form (see Crame 1981*b*), and two new genera, *Pseudomytiloides* and *Lenella*, were created to accommodate certain small, mytiliform Lower Jurassic species. It is clear from both this 1963 paper and subsequent work (e.g. Koshelkina 1969*b*), that Koshelkina recognized only these four genera of Jurassic inoceramids. Nearly all the Jurassic species previously regarded as belonging to *Inoceramus* were now taken by him to belong within *Retroceramus*. A small number of species was assigned to the other three genera, and *Inoceramus* was essentially restricted to the Cretaceous. Thus the concept of *Retroceramus*, which was originally developed to facilitate description of a distinctive group of Siberian species, was greatly expanded to cover nearly all Jurassic inoceramids.

Koshelkina (1963, 1969*b*) had obviously carefully compared his material with other faunas, for he used specific names established by other authors and his synonymies contain a number of species from both Northern and Southern Hemisphere faunas, but it was surely an ambitious claim to make that virtually all Jurassic inoceramid species could now be accommodated within the genus *Retroceramus*. There are a number of Jurassic species which seem to depart from the accepted *Retroceramus* morphology, and others which are very poorly known. In particular, it should be emphasized that, unless the hinge region of a specimen is well preserved, it is often extremely difficult to confidently assign it to *Retroceramus*. Even some Siberian Jurassic inoceramids are difficult to classify in this respect (e.g. Zakharov 1966, p. 94).

FORM AND FUNCTION IN *RETROCERAMUS*

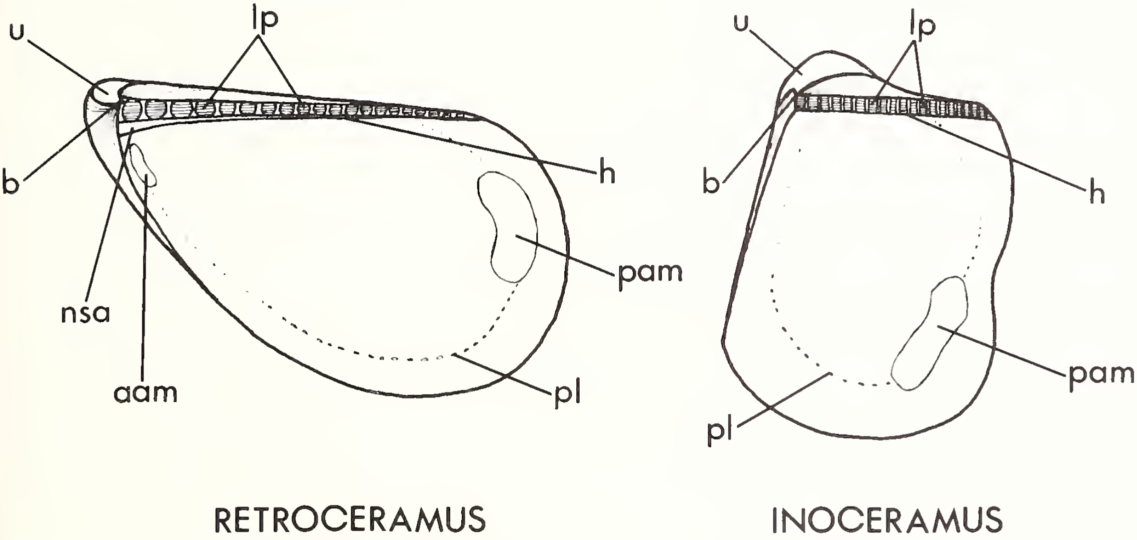
It is important to elucidate the differences between *Retroceramus* and *Inoceramus*, and establish whether these are such as to warrant the division into two separate genera. The salient features of the morphologies of *Retroceramus* and *Inoceramus* are summarized and compared in Table 1, which is largely based on descriptions and diagnoses given by Koshelkina (1963, 1969*a*, *b*) and Cox (1940, 1969).

It might appear that the two genera could be distinguished on the basis of external appearance alone, because *Retroceramus* is typically narrow and obliquely elongated, and bears simple patterns of coarse concentric ornament, while *Inoceramus* is more erect and often has much finer or irregular

TABLE 1. A comparison of the typical morphological features of *Retroceramus* and *Inoceramus*

	Retroceramus	*Inoceramus*
Equality of valves	Equivalve.	Equivalve, subequivalve, and inequivalve.
Outline	Subrhomboidal to obliquely oval; typically narrow in the region of the beak and widening uniformly towards the ventral margin; oblique elongation often results in the anterior margin lying subparallel to the posterior margin; more rounded and oval outlines are known.	Ovate, rhomboidal, or trapeziform; typically higher than long; not or only slightly oblique.
Anterior margin	Prominent anterior margins frequently developed; such margins descend steeply, but not vertically, to the plane of commissure.	Anterior margin may or may not be strongly developed; usually descending vertically to the plane of commissure.
Ornament	Characterized by large, regularly spaced concentric ribs.	Concentric ribs variably developed: more or less regularly spaced.
Wings	A low postero-dorsal wing is characteristic.	A postero-dorsal wing may or may not be present.
Beaks and umbones	Beaks typically sub-terminal; umbones opisthogyrous but occasionally prosogyrous; umbones often strongly projecting above the hingeline.	Beaks may or may not be sub-terminal; umbones generally prosogyrous and may project strongly above the hingeline.
Hingeline	Typically long and straight; edentulous.	Of variable length; edentulous.
Ligament area	Broad; bearing large, irregularly spaced ligament pits with rounded-rectangular or oval outlines; a narrow, smooth area may be present between the row of pits and the hingeline.	Narrow; bearing a uniform series of narrow, trough-like ligament pits; pits separated by thin, upstanding interspaces.
Musculature	Apparently anisomyarian, with a large posterior adductor and small anterior adductor; pallial line represented by a discontinuous series of tiny pits and depressions.	Probably consistently anisomyarian, although the musculature of *Inoceramus* is still very poorly known.
Inferred mode of life	Predominantly endobyssate.	Predominantly epibyssate, but also endobyssate and free-living.

ornament (Table 1). These broad distinctions are indeed useful, but both shell form and ornament are notoriously variable characters. Koshelkina (1963, 1969*a*) has, in fact, suggested that *Retroceramus* can also have more rounded or oval outlines, as well as reduced or irregular patterns of concentric ornament. More reliable differences may be established by recourse to certain features of the hingeline and internal shell morphology. The ligament area in particular is significantly different in the two genera (text-fig. 2). In *Retroceramus*, it is broad and typically bears large, irregularly spaced ligament pits with rounded-rectangular or oval outlines. In some instances, these pits fall into two well-defined size categories, with broad and deep ones alternating with narrower and shallower ones (e.g. Koshelkina 1963, fig. 21; 1969*a*, figs. 3 and 4). An additional feature in some species is a narrow, smooth area between the row of ligament pits and the hingeline (text-fig. 2; Koshelkina 1963, fig. 21a). In contrast, the ligament area in *Inoceramus* is comparatively narrow and the pits are markedly uniform in size and shape: narrow and trough-like in appearance, they are separated by thin upstanding interspaces (e.g. Sornay 1966, fig. 2). In *Inoceramus* the ligament area is consistently set adjacent to the hingeline (text-fig. 2).



TEXT-FIG. 2. Hinge and ligament characteristics of *Retroceramus* and *Inoceramus*. The diagrams are sketch reconstructions of internal views of typical right valves. *Key*: aam, anterior adductor muscle scar; b, beak; h, hinge; lp, ligament pits; nsa, narrow, smooth area; pam, posterior adductor muscle scar; pl, pallial line; u, umbo.

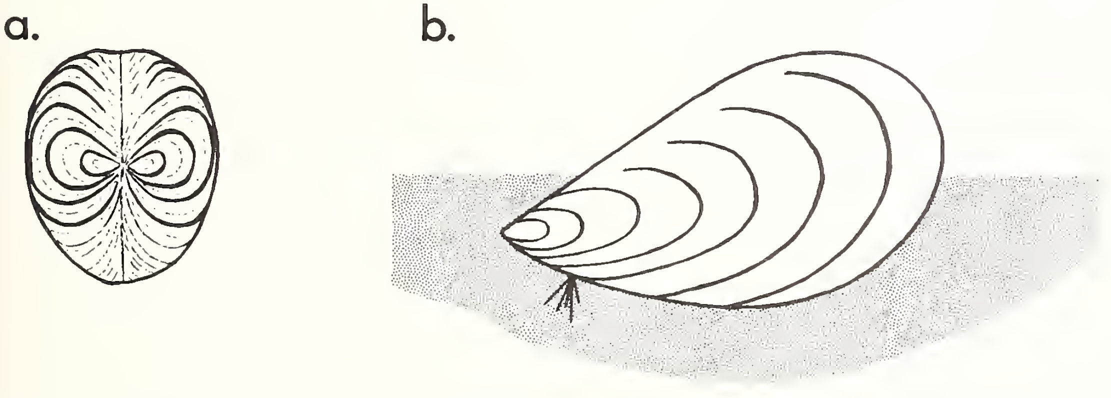
To investigate the possible functional significance of these two types of ligament it is necessary to consider the form of the valves as a whole and their life positions. Inoceramids have, of course, been extinct since the Late Cretaceous, but it is still possible to judge how they may have lived by studying the life habits and attitudes of morphologically similar living species. By such a method the probable modes of life of a number of extinct Palaeozoic bivalve genera have been reconstructed (e.g. Bambach 1971; Stanley 1972; Watkins 1978). It can be deduced from the equivalve nature of *Retroceramus* that the life position was with the sagittal plane in an essentially vertical position (with respect to a horizontal substrate). The predominantly elongated-triangular form suggests a surface-living rather than a burrowing habit, and it can be concluded that *Retroceramus* had an epifaunal life-style similar to that of many Recent Mytilidae, Isognomonidae, Pteriidae, and Carditidae (comparative data from Stanley 1970, 1972). It would also seem safe to conclude (from analogies with members of the above families) that a byssus was employed to maintain stability. The typical *Retroceramus* form, with the very anterior beaks, long opisthodetic ligament, and reduced anterior and enlarged posterior regions is, in fact, close to the classic heteromyarian form of the Mytilidae. Many common *Retroceramus* species resemble Recent mussels (see, e.g., Koshelkina 1963, 1969*a*, *b*) and it can be concluded that they had similar modes of life. Yonge (1953, 1962, 1976; also Yonge and Campbell 1968) has argued strongly that the heteromyarian condition arose as a functional response to crowded life conditions in epifaunal, byssally attached bivalves. He believes that after initial byssal attachment it was possible for bivalves to evolve by developing either their anterior or posterior regions. The former option would have offered no obvious adaptive advantages but the latter facilitated expansion of the region in which water currents were exchanged with the exterior: siphonal openings could be enlarged and significantly elevated above the crowded sea floor. The simultaneous formation of a narrow, pointed anterior also facilitated closer packing (especially by the formation of radiating clumps) and the valve was effectively streamlined to withstand strong water movements. Yonge and Campbell (1968, p. 38) emphasized that another important consequence of the evolution of the heteromyarian form was the hypertrophy of the byssal retractor muscles and their relative displacement to a position almost directly above the byssus. Stanley (1970, 1972) further stressed the importance of this structural modification, for a much stronger pull could now be exerted on the byssus and the shell very firmly clamped to the substrate. Indeed, in view of the demonstrated need of nearly all bivalves to maintain a stable position, this may be the prime reason for the evolution of a greatly expanded posterior region in so many types of epifaunal bivalve (Stanley 1970, 1972). Besides the Mytilacea, the heteromyarian form is well developed in the Dreissenacea, Carditacea, and Limacea (Yonge and Campbell 1968; Stanley 1972; Yonge 1976).

In recent years it has become increasingly apparent that many mytilid species, although byssally attached, actually live partially (or even wholly) buried within the sediment (e.g. Raup and Stanley 1978, p. 192). These forms have been termed endobyssate and can be morphologically distinguished from the true surface livers, or epibyssate species. By comparing Recent species of *Modiolus* (endobyssate) and *Mytilus* (epibyssate), Stanley (1970, 1972) has established a set of criteria by which such a distinction can be made. Endobyssate species typically have rounded-cylindrical outlines and pronounced anterior regions that are often drawn out into distinct lobes. The posterior byssal retractor muscles are situated above but well behind the byssus and the resultant force exerted by both these and the anterior retractors exerts a pull approximately parallel to the long axis of the shell: this effectively draws the shell down into the substratum. Epibyssate species, on the other hand, have more sharply triangular outlines and much reduced anterior regions. The posterior byssal retractors are inserted almost dorsal to the byssus and the resultant force exerted by these and the anterior retractors produces the strong clamping action described above. In cross-section, endobyssate species have rounded to wedge-shaped ventral margins and a maximum width at a point approximately midway between the dorsal and ventral margins. Epibyssate species have much flatter ventral surfaces and the maximum width lies close to the ventral margin (Stanley 1970, fig. 8; 1972, text-fig. 6).

Examination of some of the common *Retroceramus* species from Siberia suggests that they were very probably endobyssate. Equivalve, and with a rounded-elongate outline and evenly inflated cross-section, they would have achieved maximum stability by being at least partially buried within the substrate (text-fig. 3). Unfortunately, there is, as yet, very little evidence of the exact nature and position of the byssal opening in *Retroceramus*, but it would most likely have been a narrow slit situated in an antero-ventral position (by analogy with recent endobyssate species). *Retroceramus* probably lived with the antero-posterior shell axis inclined at an angle of anything up to 45° to the sediment surface, in a manner similar to that adopted by Recent species of *Modiolus* (text-fig. 3; Stanley 1970, fig. 7; 1972, text-fig. 3; Roberts 1975, p. 32). There are, however, some *Retroceramus* species which depart somewhat in outline and general appearance from the typical morphology (see Koshelkina 1969*a*, fig. 1). Some members of the subgenus *Fractoceramus*, such as *R.* (*F.*) *lucifer* (Eichwald) (e.g. Imlay 1955, pl. 8, fig. 7) have more angular, mytiloid outlines and could well have been epibyssate, as indeed could less obviously elongated species such as *R.* (*R.*) *polaris* (Koshelkina) (e.g. Koshelkina 1962, pl. 9, fig. 5) or *R.* (*R.*) *eximius* (Eichwald) (e.g. Eichwald 1871, pl. 18, fig. 1). Certain types with wide, flat anterior margins could also be interpreted as epibyssate, but it is apparent in all the specimens examined to date that although these prominent anterior margins drop steeply to the plane of commissure, they are not actually perpendicular to it (see Table 1). Cross-sections of whole specimens show these anterior margins to form distinct V-shaped keels rather than flat platforms (e.g. see later, text-fig. 7*a* and Pl. 57, fig. 2), and in order to maintain maximum stability these must have been at least partially buried within the substrate.

It should be possible to verify the life-style of *Retroceramus* when more is known about its musculature. In comparison with epibyssate species, endobyssate mytilids have larger anterior adductor muscles (to cope with the correspondingly larger anterior region of the shell) but somewhat smaller byssal retractors which are inserted well behind (and above) the byssal stalk (Stanley 1970, 1972). *Retroceramus* appears to have been consistently anisomyarian, with a larger postero-dorsal adductor muscle and smaller (but nevertheless still plainly visible) anterior adductor (text-fig. 2) (Koshelkina 1963, fig. 20*b*; 1969*a*, fig. 5). The musculature is probably closer to that of *Modiolus* than *Mytilus*, but so far no clear traces of the pedal-byssal muscle system have been detected.

Southern Hemisphere *Retroceramus* display morphologies essentially similar to the prodigious Siberian forms and it can be concluded that the genus as a whole was predominantly endobyssate. Some species may well have been only partially endobyssate and a few entirely epibyssate (see also descriptions and discussion, below), but on the whole the principal life habit would seem to have been within, rather than on top of, the substrate. This contrasts markedly with the inferred life habits of *Inoceramus*, which were essentially epibyssate. This genus probably had its origins well within the Jurassic but did not become widespread until the Cretaceous. Inequivalve species are particularly common in the Early Cretaceous, and it is clear that these must have lived on top of the substrate with the sagittal plane either inclined or horizontal. Species with straight, shelf-like anteriors (where the anterior valve margins do drop perpendicularly to the plane of commissure) are also prominent, and later on in the Cretaceous there are a number of large, disc-like and heavy-shelled forms that rested on the sea floor without any obvious means of attachment (data from Woods 1912; Sornay 1966; Kauffman 1968). Some Cretaceous species, and in particular a number of elongated forms in the Late Cretaceous, were probably endobyssate (see, e.g., Stanley 1972, text-fig. 23), but these are thought to be types that secondarily reverted back to a semi-infaunal mode of life. In any event, available evidence indicates that a fundamental transition occurred in inoceramid life-styles at approximately the Jurassic–Cretaceous boundary. Here, predominantly



TEXT-FIG. 3. The presumed mode of life of *Retroceramus*. *a*, anterior view of a typical *Retroceramus* showing the well-rounded ventral margin. *b*, sketch reconstruction of the same specimen partially buried within soft sediment and anchored by an antero-ventral byssus.

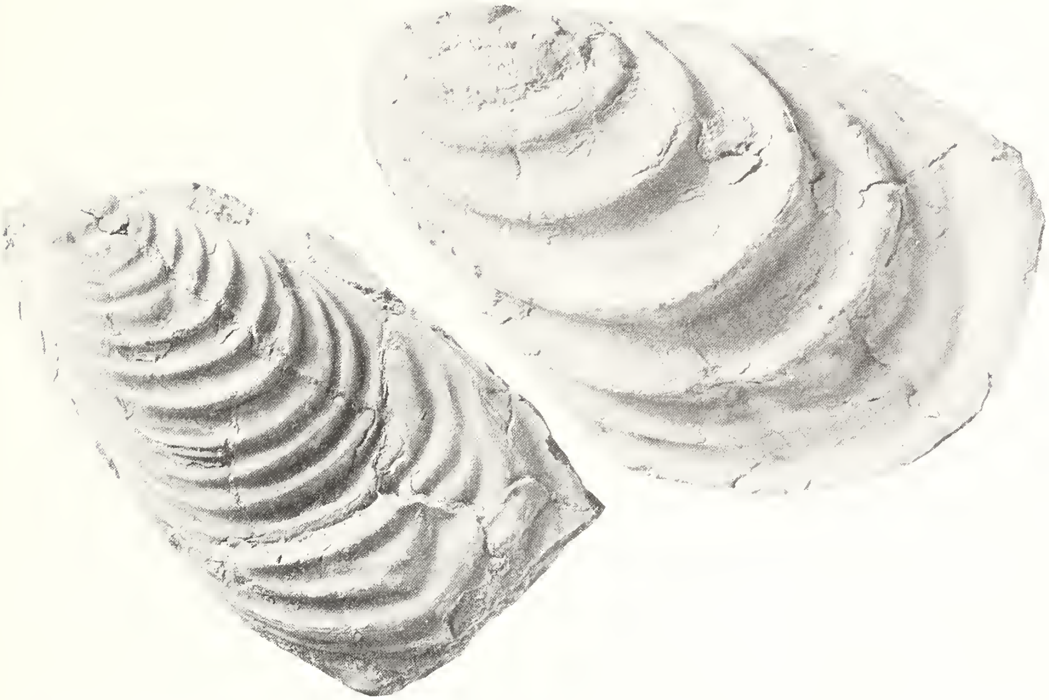
equivalve, endobyssate species of *Retroceramus* were replaced by a mixture of equivalve, subequivalve, and inequivalve epibyssate species of *Inoceramus*. Internal changes must have accompanied these pronounced changes in external shell morphology, and it would appear that the most important of these was in the structure of the ligament area. Whereas *Retroceramus* is characterized by large, rounded, somewhat irregular ligament pits, *Inoceramus* typically has a more uniform series of narrow, elongated pits. Indeed, it may be that the evolution of the *Inoceramus* grade of ligament permitted full exploitation of epibyssate habits for the first time. Perhaps shallower water (even intertidal) environments could now be colonized and the potential ecological range of the family considerably expanded. Other internal changes (such as in the musculature) undoubtedly occurred at this time too, but these have yet to be elucidated.

SOUTHERN HEMISPHERE JURASSIC INOCERAMIDS

Taking all the above points into consideration, it can be concluded that there probably are good grounds for separating *Retroceramus* from *Inoceramus* at the generic level: their respective hinge and ligament areas are fundamentally different in structure. Of course, it must be emphasized that our knowledge of the internal morphology of all inoceramids is limited, and in particular there is still very little detailed information available for Jurassic species as a whole. Nevertheless, some corroborative evidence on the structure of the *Retroceramus* ligament area will be presented below from Southern Hemisphere species. Koshelkina's (1963) three subgenera (*Retroceramus*, *Fractoceramus*, and *Striatoceramus*) can still be retained as valid subdivisions of the genus *Retroceramus*.

However, whether all the Jurassic species previously regarded as belonging to *Inoceramus* can now be directly transferred to *Retroceramus* (*sensu* Koshelkina 1963, 1969*b*) is uncertain. It has already been argued that at least a small number of species probably belong to *Mytiloides* Brongniart and *Mytiloceramus* Rollier respectively, and these have traditionally been regarded as subgenera of *Inoceramus* (see Cox 1969, p. N317). Nevertheless, casual observations of a number of specimens suggest that both these subgenera were probably functionally endobyssate and species such as *I.* (*Mytiloceramus*) *polyplocus* (Aalenian–Bajocian) and *I.* (*Mytiloides*) *fuscus* (Aalenian–?Bajocian) may yet be shown to have greater affinities with *Retroceramus*. It should be re-emphasized, though, that the hinge region of these and nearly all other European Middle Jurassic inoceramids is poorly known. Some Late Jurassic European species, such as *I. nitescens* Arkell (Oxfordian), *I. inoceramoides* (Hudleston) (Oxfordian) (see Arkell 1933, pl. 28, figs. 1–3), and *I. expansus* Blake (Kimmeridgian) (see Blake 1875, pl. 12, fig. 7), at first sight seem to show greater allegiance to *Inoceramus* than *Retroceramus*, but again there is very little precise information available on their internal shell morphologies. The view taken here is that during the Middle and Upper Jurassic there were probably two distinct inoceramid stocks, represented by the genera *Retroceramus* and *Inoceramus*, respectively. The former was more abundant, especially in temperate realms, and it was not in fact until the Early Cretaceous that *Retroceramus* was superseded by *Inoceramus*. *Anopaea* Eichwald is another valid Late Jurassic genus (Crame 1981*b*), but *Arcticeramus* Koshelkina has a somewhat doubtful status. The hinge region of *Arcticeramus* has never been adequately described (Zakharov 1966, p. 94), and it may be that the species assigned to the genus (*A. arcticus* Koshelkina, *A. eichwaldi* Koshelkina, and *A. maedae* (Hayami)) are no more than early inequivalve representatives of the genus *Inoceramus*.

Two very distinctive groups of inoceramids, based on *I. haasti* Hochstetter 1863 and *I. galoi* Boehm 1907, respectively, have traditionally been recognized in Southern Hemisphere Late Jurassic faunas. *Inoceramus haasti* is medium to large in size, sub-erect to obliquely elongated, and shows a characteristic regular expansion of the valves in a ventral direction. However, its most distinctive feature is its concentric ornament, which consists of large, simple, regularly spaced ribs separated by wide and deep interspaces (text-fig. 4*b*). Originally described from New Zealand (Hochstetter 1863), *I. haasti* has subsequently been definitely identified from Indonesia (Wandel 1936) and Antarctica (Thomson and Willey 1972), and tentatively identified from Timor (Krumbeck 1923) and New Guinea (Skwarko 1967). *Inoceramus galoi*, an Indonesian species, is also medium to large in size and obliquely elongated, but it has a narrower form than *I. haasti* (text-fig. 4*a*). It, too, has



TEXT-FIG. 4. *Retroceramus* (*Retroceramus*) *galoi* (Boehm) and *R.* (*R.*) *haasti* (Hochstetter). *a* (left), internal mould of a left valve of *R. galoi* from a locality along the Whakapirau Road, south side of Kawhia Harbour, S.W. Auckland, New Zealand (M. R. A. Thomson collection, Cambridge). *b* (right), internal mould of a left valve of *R. haasti* (BMNH L.48032) from Kohai Point, Kawhia Harbour, New Zealand (specimen illustrated by Trechmann 1923, pl. 15, fig. 3). Both specimens ×1.

prominent concentric ribs but these are more rounded in cross-section and set closer together; as a rule, the width of the interspaces is approximately equal to that of the ribs (text-fig. 4*a*). This species has also been recognized in New Zealand (e.g. Trechmann 1923; Marwick 1953) and Antarctica (Quilty 1977), and tentative occurrences have been recorded from Japan (Hayami 1960), New Guinea (Glaessner 1945), New Caledonia (Avias 1953; Freneix, Grant-Mackie and Lozes 1974), and South America (Stehn 1924; Giehm 1960; Harrington 1961). Although believed to be Oxfordian in age in Indonesia by Wandel (1936), both these species have been consistently dated as Kimmeridgian in New Zealand (*I. galoi* being Heterian or Lower Kimmeridgian and *I. haasti* Ohauan or Middle Kimmeridgian) (e.g. Speden 1970; Stevens and Speden 1978). In any event, *galoi* seems to occur stratigraphically beneath *haasti* in both areas, and many workers have taken the two species to be end members of a morphological series. This belief was strengthened by the occurrence in New Zealand of transitional forms that showed an ornament pattern intermediate between that of *galoi* and *haasti*. These specimens were identified by J. B. Waterhouse (*in* Fleming and Kear 1960, p. 43) as *I.* cf. *subhaasti* Wandel, and the idea quickly became established that the latter species was a morphological intermediate between the two distinctive end members. The concept of a *galoi–subhaasti–haasti* evolutionary lineage has been widely promulgated (Fleming 1958; Fleming and Kear 1960; Stevens 1968; Speden 1970; Spörli and Grant-Mackie 1976; Glaessner 1945; Freneix *et al.* 1974).

Although members of the *galoi–subhaasti–haasti* group of species have always been regarded as belonging to the genus *Inoceramus*, there is considerable evidence to suggest that they should now be transferred to *Retroceramus*. In particular, *I. galoi* appears to show many of the typical *Retroceramus* features outlined above. In addition to its narrow, obliquely elongated form and strong concentric ornament, it clearly has a long, straight hinge and a smooth anterior margin that drops steeply to the plane of commissure (text-fig. 4*a*; Trechmann 1923, pl. 15, figs. 1 and 2;

Wandel 1936, fig. 2; Marwick 1953, pl. 12, fig. 2; Speden 1970, figs. 38 and 39; Quilty 1977, figs. 23 and 24). The hinge region of the type specimen is incomplete (Boehm 1907, pl. 10, fig. 1), but it would seem from an examination of some of the prolific New Zealand material (from south-west Auckland) that adult specimens typically have a low postero-dorsal wing (e.g. text-fig. 4*a*; see also Trechmann 1923, pl. 15, fig. 1). Most characteristic, however, is the presence of large ligament pits that can be grouped into two distinct size classes (Wandel 1936, p. 466; Boehm 1907, pl. 9, fig. 10). Indeed, in almost all respects, *I. galoi* is very close to *I. retrorsus* Keyserling, the type species of the genus *Retroceramus* (Boehm 1907, p. 69; Kruizinga 1926, p. 19; cf., e.g., Lahusen 1886, pl. 1, fig. 1, Koshelkina 1963, pl. 6, fig. 2a, and text-fig. 4*a*).

The description and illustrations of *I. haasti* given by Wandel (1936, figs. 4, 5*a* and *b*; pl. 19, figs. 1*a*–*c*; pl. 20, figs. 1 and 2) indicate that this species, too, has strong affinities with *Retroceramus*. Obliquely elongated and exhibiting prominent concentric ornament, it also has valves with a low postero-dorsal wing and a well-demarcated anterior margin. The ligament pits appear to be of more uniform size than those of *galoi*, but are separated by broad interspaces. The ligament region as a whole seems to be considerably thickened (Wandel 1936, p. 475). *Inoceramus haasti* has been directly compared with both *I. retrorsus* var. *tongusensis* Lahusen (1886, pl. 1, fig. 2; Kruizinga 1926, p. 19) and the North American species, *R. ferniensis* (Warren) (Wandel 1936, p. 467). *Inoceramus subhaasti* Wandel is a smaller, more variable species, but again shows good *Retroceramus* features. The obliquely elongated to subquadrate outline and prominent postero-dorsal wing are particularly reminiscent of some of the smaller Siberian *Retroceramus* species. Wandel (1936, p. 472) believed his *I. subhaasti* var. *denseplicata* to be very close to *I. retrorsus* Keyserling.

A note of caution should perhaps be introduced here, for it is obvious that some confusion exists as to the precise identity of each of these three species. In the past there has been a tendency to allocate Southern Hemisphere Late Jurassic species to *galoi* if the concentric ribs are set close together, *haasti* if they are set far apart, and *subhaasti* if they are intermediate in density: other diagnostic criteria have often been largely ignored. Specimens from both Japan and the Philippines have been assigned to the *I. galoi* group by Hayami (1960, p. 307, pl. 16, fig. 6; 1968, p. 174, pl. 21, figs. 1–3), but these differ in several important respects from the well-known Indonesian and New Zealand material. Similar departures from the accepted *galoi* morphology are shown by at least some of the South American specimens currently assigned to the species (e.g. Stehn 1924, pl. 5, figs. 4 and 5). Further pronounced differences can be found between illustrated specimens of *I. haasti* from south-west Auckland, New Zealand. Zittel's (1864, pl. 8, figs. 5*a* and *b*) figures show the species to be erect, prosogyrous, and to have bilaterally symmetrical ornament: Trechmann's (1923, pl. 15, fig. 3; text-fig. 4*b*) specimen is clearly obliquely elongated, but Marwick's (1953, pl. 12, fig. 1) hypotype is again sub-erect and has symmetrical ornament. Clearly, the prime criterion for the identification of *haasti* in New Zealand has been the nature of the ornament, and little consideration has been given to the overall form of the valves. Similarly, a specimen assigned to *I.* cf. *subhaasti* from New Zealand (NZGS 9932, text-fig. 7*a*; here identified as *Retroceramus* (*Retroceramus*) sp. nov. 2—see below) has an intermediate rib density, but shows a number of marked differences in valve form from Wandel's (1936) type material. These specific distinctions have important taxonomic, biogeographic, and evolutionary implications, and will be discussed in more detail in the systematic section below.

Some of the poorly preserved medium to large, coarsely ribbed inoceramids from Indonesia, Himalayas (Spiti), and New Caledonia can also be tentatively referred to *Retroceramus*. Boehm's (1907) Indonesian species, *I. sularum* and *I. taliabuticus*, may perhaps belong within the *I. haasti* group (Kruizinga 1926; Wandel 1936) or, alternatively, be distinct species of *Retroceramus* in their own right (e.g. Koshelkina 1969*b*, p. 80 refers to *R. sularum* (Boehm)). It must be emphasized, however, that both these species are based on single, poorly preserved specimens. *Inoceramus sularum* may also be present in the Spiti Shales, but the specimen described by Holdhaus (1913, p. 421) is both worn and incomplete. *Inoceramus hookeri* Salter from the Spiti Shales has a rounded-rectangular outline, prominent concentric ornament, and a low, impressed postero-dorsal wing (Salter and Blanford 1865, pl. 23, fig. 1). Traces of broad ligament pits suggest greater affinities with *Retroceramus* than *Inoceramus*, but the species is known only from a single incomplete specimen. *Inoceramus hookeri* var. *crenatulinus* Salter (*in* Salter and Blanford 1865, pl. 23, fig. 2) belongs within *R. everesti* (Oppel) (see below).

Inoceramids from the Late Jurassic deposits of New Caledonia were interpreted by both Avias (1953) and Routhier (1953) within the concept of the *galoi-subhaasti-haasti* lineage, but owing to their poor state of preservation no positive identifications were possible. It will be pointed out below that some, at least, of their specimens may represent new and as yet undescribed species of *Retroceramus*: the specimens identified as *I.* cf. *subhaasti* by Avias (1953, pl. 23, fig. 3) and Routhier (1953, pl. 2, fig. 9) may be new species within the subgenus *Retroceramus* (*Retroceramus*), and Routhier's (1953, pl. 2, fig. 8) *Inoceramus* sp. could be a small *Fractoceramus*.

Two New Zealand Middle Jurassic species, *I. inconditus* Marwick and *I. brownei* Marwick, can also be reclassified within *Retroceramus*. The former of these two belongs within the subgenus *Fractoceramus*, and there are strong resemblances to Siberian species such as *R.* (*F.*) *lungerhauseni* Koshelkina (e.g. Koshelkina 1962, pl. 9, fig. 1; 1963, pl. 13, fig. 1) and *R.* (*F.*) *elegans* Koshelkina (e.g. Koshelkina 1962, pl. 9, fig. 4; 1963, pl. 12, fig. 2). Koshelkina (1969*b*, p. 75) identified the other species, *I. brownei*, as a *Retroceramus*, but did not assign it to a subgenus. A third New Zealand species, *I. marwicki* Speden, may possibly have *Retroceramus* affinities too. At first sight it would appear to be a typical *Inoceramus*, being small and erect, and possessing only faint concentric ornament. However, Speden (1970, p. 848) has suggested that *marwicki* may be a transitional species in an evolutionary lineage from *I. brownei* to *I. galoi*, both of which can now be assigned to *Retroceramus*: small, faintly ornamented species of this genus are known from Siberia (e.g. *R. elatus* Koshelkina (1969*b*, p. 53, pl. 8, figs. 1-5)).

To sum up, there is good evidence to show that the genus *Retroceramus* is well represented in the extensive Late Jurassic deposits of the Southern Hemisphere. *Anopaea* is also present (Crame 1981*b*), but there are apparently very few true members of the genus *Inoceramus*.

SYSTEMATIC DESCRIPTIONS

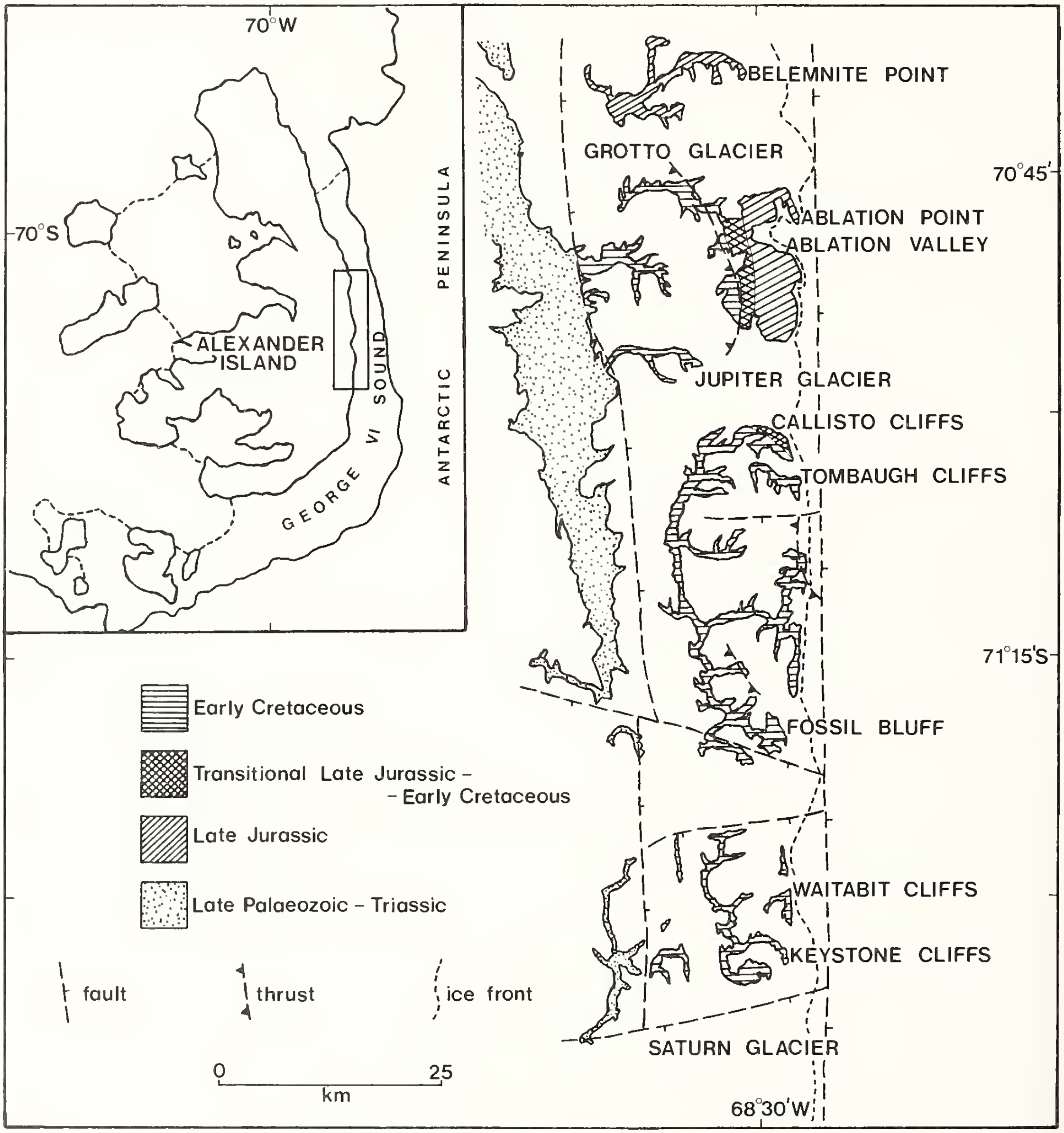
The poor state of preservation of so many Southern Hemisphere Late Jurassic inoceramids has consistently hampered detailed systematic studies. Collections from certain localities consist of no more than a small number of incomplete specimens, and many diagnoses have necessarily been based on very limited material. In only a few instances has it been possible to fully assess the range of morphological variation within and between closely related species. In an attempt to remedy this situation for the Antarctic Peninsula, a programme of intensive bed by bed collecting has been carried out in the Mesozoic Fossil Bluff Formation of eastern Alexander Island (text-figs. 1 and 5; see Taylor *et al.* 1979), and a similar programme has recently been initiated in the Latady Formation of the Lassiter and Orville coasts (Thomson *et al.* 1978).

At present, only one species from the Antarctic Peninsula, *Retroceramus everesti* (Oppel), is known from a comparatively large number of specimens (see below). Other well-known Southern Hemisphere species, such as *R. haasti* and *R. subhaasti*, are represented in the collections, but only in the form of broken or poorly preserved material. There are also several new species, but as these are all based on very limited material they have not been formally named. Instead, a system of open nomenclature has been adopted whereby material likely to represent a new species has been designated by a number (e.g. *Retroceramus* sp. nov. 1), and that resembling an existing species has been designated by the prefix 'cf.'. Wherever possible, the following measurements were taken:

shell length (L)—the length of the valve as measured along the direction of maximum growth (or growth axis) (*Wachstumsrichtung* of Seitz 1935).
shell width (W)—the maximum dimension perpendicular to the length.
length of hingeline (H).

The following angles, based on a scheme devised by Hayami (1960), were also measured:
α—the angle between the hingeline and the anterior margin (the apical angle).
β—the beak angle (or angle of umbonal inflation).
γ—the angle between the hingeline and postero-dorsal margin (the postero-dorsal angle).
δ—the angle between the hingeline and direction of maximum growth (the angle of obliquity).

The prefixes BMNH and NZGS denote specimens held in the British Museum (Natural History) and New Zealand Geological Survey collections, respectively: all the remaining specimens are held in the collections of the British Antarctic Survey, Cambridge. The following symbols have been used in the tables of measurements: LV—left valve, RV—right valve, *—approximate value.



TEXT-FIG. 5. Geological map of the central east coast of Alexander Island. The Fossil Bluff Formation comprises the Late Jurassic to Early Cretaceous strata.

Family INOCERAMIDAE Giebel, 1852
Genus RETROCERAMUS Koshelkina, 1963
Subgenus RETROCERAMUS (RETROCERAMUS) Koshelkina, 1963
Retroceramus (*Retroceramus*) *haasti* (Hochstetter, 1863)

Plate 57, figs. 1–4

1863 *Inoceramus haasti* Hochstetter, p. 190.
1864 *Inoceramus haasti* Hochstetter; Zittel, p. 33, pl. 8, figs. 5*a–c*.
1923 *Inoceramus haasti* Hochstetter; Trechmann, p. 275, pl. 15, fig. 3.
1923 *Inoceramus* sp. cf. *haasti* Hochstetter emend. Zittel; Krumbeck, p. 78, pl. 173, fig. 13.
1936 *Inoceramus haasti* Hochstetter emend. Zittel; Wandel, p. 573, text-figs. 4 and 5, pl. 19, fig. 1 and pl. 20, figs. 1 and 2.
1953 *Inoceramus haasti* Hochstetter; Marwick, p. 91, pl. 12, fig. 1.
(?)1967 *Inoceramus* sp. cf. *haasti* Hochstetter; Skwarko, p. 68, pl. 10, figs. 5 and 6.
1972 *Inoceramus haasti* Hochstetter; Thomson and Willey, p. 1, fig. 2.

Material. One broken internal mould (KG.701.74) from Ablation Valley, eastern Alexander Island (text-fig. 5), and an incomplete external mould (BMNH LL.10015) which probably comes from a moraine approximately 1·7 km north of Ablation Point.

Measurements. Comparative measurements are also given for the specimens illustrated by Trechmann (1923) (BMNH L.48032; text-fig. 4*b*) and Marwick (1953) (spec. no. TM.2374), and specimen BMNH LL.24175 (Pl. 57, figs. 1, 2).

Specimen number	L (mm)	W (mm)	W/L	H (mm)	α	β	γ	δ
KG.701.74 (LV)	120*	72	0·60	—	62°*	—	—	45°*
L.48032 (LV)	100*	61	0·61	—	46°	40°*	—	32°*
TM.2374 (LV)	104	63	0·61	—	62°*	—	—	—
LL.24175 (LV)	92*	47*	0·51	—	42°*	40°	—	36°
LL.24175 (RV)	87*	56*	0·64	45*	59*	48°	142*	50°

Remarks. Thomson and Willey (1972, p. 1) based their identification of *I. haasti* on a broken internal mould of a medium sized left valve (KG.701.74). The umbonal and hinge regions of this specimen are missing, but it can be judged to have been obliquely elongated and considerably expanded towards the ventral margin (Thomson and Willey 1972, fig. 2; Pl. 57, fig. 3). It bears the sharp, widely spaced concentric ribs that are so typical of this species and compares well with specimens of *I. haasti* illustrated by both Trechmann (1923, pl. 15, fig. 3; text-fig. 4*b*) and Wandel (1936, text-fig. 4 and pl. 20, fig. 1).

It should be emphasized again here that this is a species characterized primarily by its distinctive style of ornament: little attention has been paid so far to the form of the valves. Specimens from both New Zealand and Indonesia suggest that the valve outline varies from sub-erect to obliquely elongated (see p. 566 and Wandel 1936, text-figs. 4 and 5, pl. 20, figs. 1 and 2; pl. 21, figs. 1*a–c*), and it is likely that this is due to both original intraspecific variation and some degree of post-mortem distortion. A specimen from Kowhai Point, south-west Auckland, New Zealand (BMNH LL.24175, Pl. 57, figs. 1, 2) clearly shows how the latter can considerably affect the interpretation of valve morphology. This specimen, which is medium sized and moderately inflated, is noteworthy for the very prominent anterior margins on both valves. These are smooth and flat, and descend steeply (but not vertically) for a distance of approximately 3 cm to the plane of commissure. The right valve (Pl. 57, fig. 2) is apparently sub-erect and prosogyrous, although there are indications that the postero-dorsal area may originally have been more extensive. In contrast, the left valve (Pl. 57, fig. 1), although less complete, gives the appearance of having been narrower and more oblique. The valves of this specimen have been sheared and slightly crushed, and its exact form is hard to establish: the right valve seems to be erect and prosogyrous, and the left narrow and obliquely elongated (Pl. 57, figs. 1, 2). Inspection of Wandel's (1936) illustrations shows similar variation from slightly prosogyrous (e.g. Wandel 1936, pl. 20, fig. 2) to opisthogyrous forms (e.g. Wandel 1936, text-fig. 4), but there is no consistent variation between the right and left valves.

Specimen BMNH LL.10015 from Alexander Island is a poorly preserved external mould of a large left valve bearing prominent concentric ribs of the *haasti* type (Pl. 57, fig. 4). The precise form of the valve is indeterminate, but it can be judged from the course of the ribs to have been obliquely elongated and ventrally expanded. A broken external mould of a small right valve from Low Island, South Shetland Islands (text-fig. 1), can also be tentatively referred to *R. haasti* (M. R. A. Thomson, pers. comm.).

Early evidence suggested that *R. haasti* was of Oxfordian age in Misol, East Celebes, and New Zealand (Wandel 1936, pp. 517–518). However, subsequent work on associated molluscan faunas placed the Ohauan stage, in which *R. haasti* occurs in New Zealand, in the Middle Kimmeridgian (Fleming 1958; Fleming and Kear 1960), and also suggested that the Misol occurrence may be as late as Lower Tithonian (Stevens 1965, p. 139). Thomson and Willey (1972, p. 17) lent some support to the earlier view of an Oxfordian age for *R. haasti*, as their specimen from Ablation Valley apparently comes from the same stratigraphical level as an Upper Oxfordian–Lower Kimmeridgian ammonite, *Perisphinctes* (*Orthosphinctes*) cf. *transatlanticus* (Steinmann) (Howarth 1958). This level, which occurs at the base of the Ablation Valley section (see later, text-fig. 9), is a sequence of slumped clastic sediments (known as the 'disturbed zone') whose precise age has yet to be established (Elliot 1974, p. 92) (see discussion section, below). Belemnites collected from the zone suggest an Upper Oxfordian–Middle Kimmeridgian age (Willey 1973), but it is apparent that all the fossils were collected from associated scree deposits rather than *in situ*. The occurrence of the top of the disturbed zone less than 100 m beneath a distinctive Tithonian ammonite fauna (text-fig. 9) (see p. 590) strongly suggests that at least part of the zone may range up into the Tithonian. Support for a Tithonian, or at least Kimmeridgian–Tithonian, age for *haasti* comes from more recent investigations in both Indonesia and New Zealand. Westermann *et al.* (1978) have identified *R. haasti* from near the top of a Kimmeridgian–Middle Tithonian sequence in the Sula Islands, Indonesia, and Stevens and Speden (1978) have indicated that one tenable interpretation of the New Zealand Jurassic ammonite faunas places the entire Ohauan stage in the Upper Tithonian (see discussion section, below). A Middle Kimmeridgian–Tithonian age range is accepted here as more likely for *R. haasti* than an Oxfordian–Kimmeridgian one.

There are strong similarities between *R. haasti* and certain Middle Jurassic Boreal species of *Retroceramus*. The more elongate forms of *haasti* (e.g. Wandel 1936, text-fig. 4), for example, are close to *R.* (*R.*) *elongatus* Koshelkina (e.g. Koshelkina 1963, pl. 15, fig. 4), and the squatter, more erect forms (e.g. Wandel 1936, pl. 19, fig. 1*a*) to types such as *R.* (*R.*) *marinus* Koshelkina (e.g. Koshelkina 1969*b*, pl. 21, fig. 1). Koshelkina (1969*b*, p. 76) has in fact suggested that Krumbeck's (1923) *I.* cf. *haasti* could be included within another Middle Jurassic species, *R.* (*R.*) *morosus* Koshelkina, but this identification is thought to be in error. As discussed above, Krumbeck's (1923, pl. 173, fig. 13) specimen of *I.* cf. *haasti* seems to be close to a number of other *haasti* specimens,

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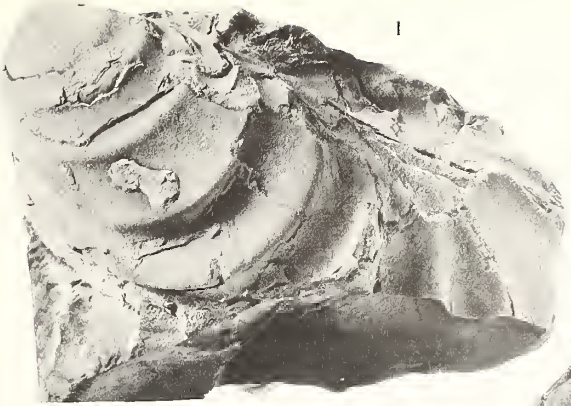
EXPLANATION OF PLATE 57

Figs. 1–4. *Retroceramus* (*Retroceramus*) *haasti* (Hochstetter). 1, internal mould (with traces of shell material) of a whole specimen (BMNH LL.24175) viewed from the left side; from a locality near Kowhai Point, Kawhia Harbour, S.W. Auckland, New Zealand. 2, the same specimen viewed from the right side. 3, incomplete internal mould of a left valve (KG.701.74) from the south side of Ablation Valley, Alexander Island. 4, latex peel from an external mould of an incomplete left valve (BMNH LL.10015) from a moraine approximately 1·7 km north of Ablation Point, Alexander Island.

Figs. 5–6. *R.* (*R.*) *haasti* (Hochstetter) juv. (?). 5, internal mould of two incomplete single valves (KG.728.11) from a moraine approximately 1·7 km north of Ablation Point. 6, an internal mould of an incomplete single valve (KG.728.10) from the same locality. All specmens ×1.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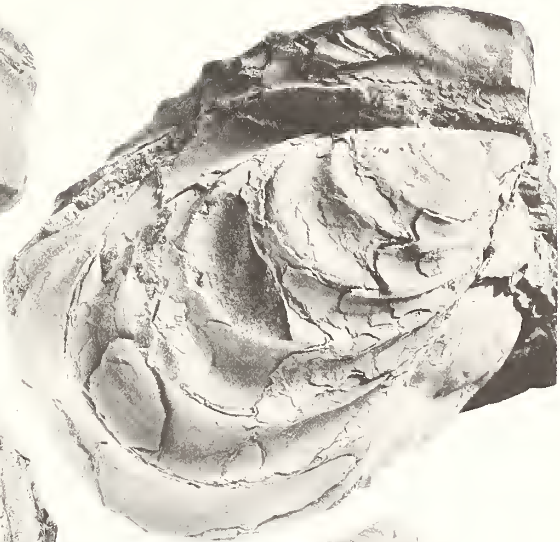
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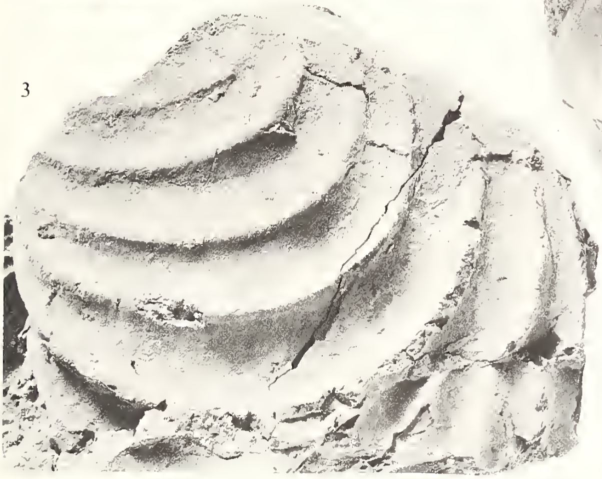
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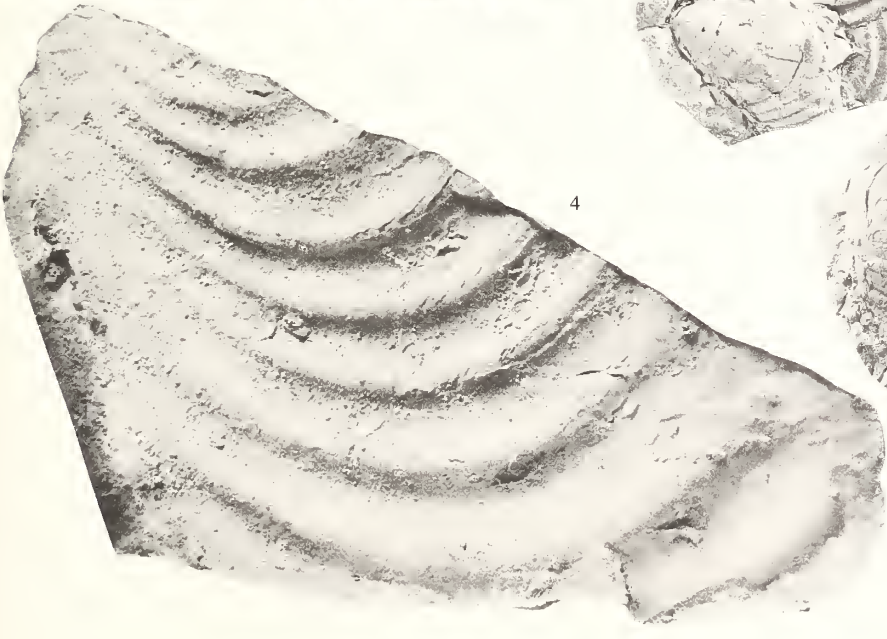
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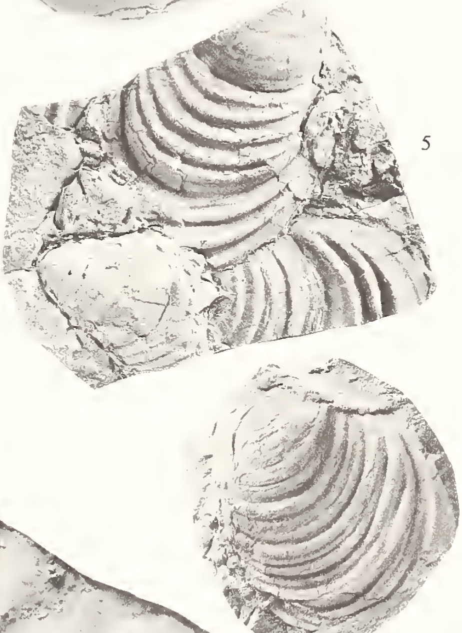
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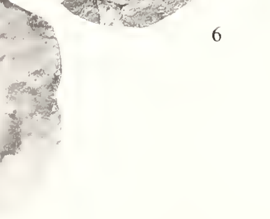
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CRAME, Inoceramid bivalves

and it would seem more appropriate to retain it within this species than to refer it to a less well-known Middle Jurassic Siberian species. That there is a strong similarity, especially in style of ornament, between species such as *haasti*, *elongatus*, and *morosus* is not disputed, but it is apparent that there are subtle differences between them in valve form and outline. This may indeed be no more than a striking example of homeomorphy between Middle and Late Jurassic species.

Retroceramus (*Retroceramus*) *haasti* (Hochstetter) juv. (?)

Plate 57, figs. 5, 6

1972 *Inoceramus* sp. δ; Thomson and Willey, p. 5, fig. 4*b*.

Material. Three incomplete internal moulds (KG.728.10 and 11) from a moraine approximately 1·7 km north of Ablation Point, eastern Alexander Island.

Description. The approximate dimensions of two of these specimens are 45 mm (length) by 30 mm (width), and of the third, 55 by 27 mm. They are all compressed and have incomplete margins. All three specimens are characterized by inflated umbonal regions that are clearly differentiated from the main body of the valve and bear traces of fine concentric ornament (Pl. 57, figs. 5, 6; Thomson and Willey 1972, fig. 4*b*). Over the rest of the valve prominent concentric ribs between 1·0 and 1·5 mm in width are developed: on the two valves on specimen KG.728.11 these ribs are evenly distributed (Pl. 57, fig. 5), but on specimen KG.728.10 they are somewhat irregular and discontinuous (Pl. 57, fig. 6). The course of the ribs suggests that all three specimens were approximately bilaterally symmetrical.

Remarks. The small size, finely ribbed umbonal stage, and regular concentric ornament suggest that these specimens may be juveniles of *R. haasti*. All three specimens compare well with probable juveniles of *I. haasti* from New Zealand (Spörli and Grant-Mackie 1976, text-figs. 10–12). A noticeable feature common to both the Antarctic and New Zealand specimens is the possession of a finely ornamented, upstanding umbonal region. Such an umbonal region seems to be a consistent feature of the juvenile stages of *R. haasti* (Wandel 1936, p. 466; Freneix *et al.* 1974, p. 462). Loose ammonites associated with specimens KG.728.10 and 11 have strong Tithonian affinities (Thomson and Willey 1972, p. 5; Thomson 1979, p. 32).

Retroceramus (*Retroceramus*) sp. cf. *subhaasti* (Wandel, 1936)

Plate 58, fig. 1

cf. 1936 *Inoceramus subhaasti* n. sp. var. *denseplicata* Wandel, p. 469, pl. 15, fig. 2, pl. 16, figs. 5*a* and *b*.
1975 *Inoceramus* cf. *subhaasti* Wandel 1936; Thomson, p. 34, fig. 3*b*.

Material. One internal mould of a single valve (KG.1258.9), preserved in fine-grained sandstone, and one whole specimen (KG.1258.66), preserved in mudstone, from Carse Point on the west coast of the Antarctic Peninsula (text-fig. 1).

Description. Specimen KG.1258.9 is a small, strongly inflated left valve with a narrow, rounded-rectangular outline (Pl. 58, fig. 1). Although the margins are incomplete and the specimen is slightly distorted, it can be judged to have been obliquely elongated. The maximum degree of inflation lies along the growth axis and there are steep descents to both the long, arcuate anterior margin and the remnants of the postero-dorsal wing (Pl. 58, fig. 1). The umbonal region is inflated and demarcated from the main body of the valve by a shallow, concentric sulcus. The umbo is twisted and in all probability projected strongly above the hingeline (Pl. 58, fig. 1). Low, rounded concentric ribs cover the valve. Between 1·0 and 1·5 mm in width, they appear to have been closely and regularly spaced over the valve surface: however, there is some evidence of crowding on the postero-dorsal wing close to the hinge margin (Pl. 58, fig. 1). The small whole specimen (KG.1258.66), although incomplete and partially distorted, has finely ribbed, strongly projecting umbones which are sharply differentiated from the more coarsely ribbed central areas of the valves (Thomson 1975, p. 34 and fig. 3*b*).

Measurements. KG.1258.9 (LV): L 53 mm, W 24 mm, W/L 0·47, α 70°*, β 32°, δ 70°*. KG.1258.66 (LV): L 42 mm, W 22* mm, W/L 0·52, α 50°*, γ 144°*.

Remarks. *Retroceramus subhaasti* is a distinctive species, characterized by a sub-quadrate outline, strongly projecting, twisted umbones, and a long, straight hinge: the style of ornament may be somewhat variable (Wandel 1936), but the valve form is consistent and definitive. Specimen KG.1258.9 appears to possess all the typical *subhaasti* features, but as the hinge and postero-dorsal area are incompletely preserved it can only be tentatively referred to this species. Judging from the styles of ornament, both it and specimen KG.1258.66 are probably closest to Wandel's (1936) *I. subhaasti* var. *denseplicata* (e.g. Wandel 1936, pl. 15, fig. 2 and pl. 16, figs. 5*a* and *b*) (see also Thomson 1975, p. 34).

Retroceramus subhaasti may be distinguished from *R. haasti* by its more quadrate outline, prominent hinge and postero-dorsal wing, and strongly projecting umbo. The two species cannot, however, be satisfactorily separated on the grounds of ornament alone, for some varieties of *subhaasti* have concentric ribs almost as strongly developed and widely spaced as those of *haasti* (e.g. Wandel 1936, text-figs. 2 and 3). Attention should also be drawn to the fact that, like *R. haasti*, *R. subhaasti* shows strong similarities to a number of Middle Jurassic species of *Retroceramus*. In particular, there are striking resemblances to members of the *R. kystatymensis* group of species (Koshelkina 1963, p. 138). *Retroceramus vagti* Koshelkina (Callovian), a prominent member of this group, has a sub-quadrate outline, very long hinge, and strong concentric ornament, and approaches in form types such as *I. subhaasti* var. *intermedia* Wandel (cf. Koshelkina 1962, pl. 10, fig. 2 and Wandel 1936, pl. 18, fig. 3*a*). However, the correspondence is not exact, and this is again thought to be nothing more than a case of homeomorphy between Jurassic species of *Retroceramus*. Associated faunas rule out any possibility of systematic equivalence between *R. subhaasti* and members of the *R. kystatymensis* group.

In Indonesia, *R. subhaasti* is particularly common in the Lilinta Marls of Misol (Wandel 1936). These beds lie directly beneath the Lower Fatjet Shales containing *R. haasti* and can probably be dated as Middle Kimmeridgian (Stevens 1965, p. 139). *Retroceramus subhaasti* also occurs in the Sula Islands, but its stratigraphical position there is less certain. Most of the early specimens were collected loose from stream beds and there is no clear indication of stratigraphical separation between *R. subhaasti* and *R. galoi* (Wandel 1936, pp. 517–519). More recent collections suggest that *R. galoi* occurs both above and beneath *R. subhaasti*, and that both these species occur stratigraphically below *R. haasti* (Westermann *et al.* 1978, p. 98). *Retroceramus galoi* has an apparent range of Middle Oxfordian–Kimmeridgian and *R. subhaasti* of (?) Upper Oxfordian–Lower Kimmeridgian. However, systematic and stratigraphical studies are not yet complete in the Sula Islands (Westermann *et al.* 1978) and these ranges should only be regarded as tentative. Associated ammonites and belemnites date the sedimentary sequence from which specimens KG.1258.9 and 66 were obtained as Late Jurassic (Thomson 1975). Current interpretations of those genera and species present favour a Middle–Upper Tithonian age, but it is possible that this range may eventually be extended down into the Kimmeridgian (Thomson 1975, p. 41). At present, it would seem best to assign *R. subhaasti* only to an undifferentiated Middle Kimmeridgian–Tithonian age range.

Retroceramus everesti group

During recent field-work, a large number of inoceramid specimens with a distinctive ornament pattern of fine, closely spaced concentric ribs was collected from a thick Late Jurassic–Early Cretaceous section at Callisto Cliffs, eastern Alexander Island (text-fig. 5). Although predominantly incomplete or deformed, many of these specimens seemed to show close affinities with *I. everesti* Oppel (see Holdhaus 1913, pp. 415–417, pl. 98, figs. 12–14). Further investigations confirmed this similarity, and indicated that a number of other Late Jurassic–Early Cretaceous Southern Hemisphere inoceramids could also be linked to this distinctive species group. It would seem, in fact, that the *everesti* group is particularly common in Southern Hemisphere Jurassic–Cretaceous boundary beds. As such, it is potentially very useful for regional biostratigraphical correlations.

It will become apparent from the descriptions and discussions below that substantial morphological variation has been allowed within the *everesti* group: indeed, it is possible that several distinct subspecies may eventually be established within it. However, at present only one distinct morphological subgroup can be recognized. This is a group of small, finely ribbed specimens which occur at the base of the *everesti* zone at Callisto Cliffs: these specimens appear to be evolutionary precursors of *everesti, sensu stricto*, and are separated off here as a distinct variety, *R. everesti* var. *α*. As this variety occurs stratigraphically beneath *R. everesti* proper, it is described first below. Throughout the following descriptions emphasis will be placed on stratigraphical changes in morphology as seen in the Callisto Cliffs section.

Retroceramus (*Retroceramus*) *everesti* (Oppel) var. *α*

Plate 58, figs. 2-4

Material. Six incomplete single valves from the base of the Callisto Cliffs section, eastern Alexander Island. The collection consists of two external (KG.2802.32 and 319) and two internal (KG.2802.132 and 282) moulds of right valves, and one internal (KG.2802.230) and one external (KG.2802.286) mould of a left valve. All specimens are preserved in siltstone.

Description. The stratigraphically lowest specimen (KG.2802.32) is a small, obliquely elongated, external mould of a left valve: its length is approximately twice the maximum width. A latex peel shows the specimen to have been moderately convex, with the maximum degree of inflation occurring in the umbonal region and along the growth axis (Pl. 58, fig. 2). There are smooth descents from the latter to both the anterior margin and the long, straight hingeline. The posterior and ventral margins are incomplete, but are judged to have been well rounded (Pl. 58, fig. 2). The umbonal region is distinct, and the beak would appear to have been terminal. A long, low, postero-dorsal wing is distinct at its anterior end but posteriorly merges discretely into the main body of the valve (Pl. 58, fig. 2). The ornament pattern on specimen KG.2802.32 consists of a single set of low, rounded concentric ribs which are less than 1 mm in width and lie slightly asymmetrically about the growth axis (Pl. 58, fig. 2). In places these ribs are adjacent, but elsewhere they are separated by narrow, flat interspaces. The ribs tend to coalesce and become finer towards both the wing and the anterior margin: they are noticeably finer over the umbo (Pl. 58, fig. 2).

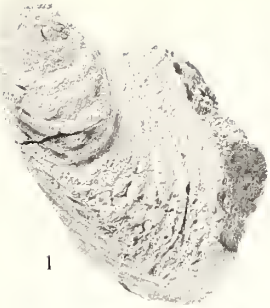
Specimens KG.2802.132 and 282 agree well with KG.2802.32. Specimen KG.2802.132 is particularly close, differing only in its larger size and slightly finer ornament (Pl. 58, fig. 3). Unfortunately, this specimen was collected from a small scree fan (one of only a few such specimens), and its exact level of origin is unknown. Specimen KG.2802.319, an incomplete external mould of a left valve, is slightly larger and more erect than the previous three specimens. Noticeably broader, it has distinct concentric ribs (1 mm wide and separated by similar-sized interspaces) developed towards the ventral margin. These seem to fuse into ill-defined groups towards the umbo, and become much finer on the flat postero-dorsal wing. This specimen may be a transitional form between the var. *α* and the main *everesti* group.

EXPLANATION OF PLATE 58

Fig. 1. *Retroceramus* (*Retroceramus*) sp. cf. *subhaasti* (Wandel). Internal mould of a left valve (KG.1258.9) from Carse Point on the west coast of the Antarctic Peninsula.

Figs. 2-4. *R.* (*R.*) *everesti* (Oppel) var. *α* from Callisto Cliffs, Alexander Island. 2, latex peel from an external mould of a left valve (KG.2802.32). 3, internal mould of a left valve (KG.2802.132). 4, incomplete internal mould of a right valve (KG.2802.230).

Figs. 5-11. *R.* (*R.*) *everesti* (Oppel). 5, incomplete internal mould of a right valve (with traces of shell material) (KG.2803.112). 6, latex peel from an external mould of a right valve (KG.2802.655a). 7, internal mould of a large right valve (partly covered by a thin shell layer) (KG.2802.384). 8, latex peel from an external mould of an incomplete right valve (KG.2803.655b). 9, internal mould of a more erect right valve (KG.2802.544). 10, latex peel from an external mould of an incomplete right valve (KG.2802.462). 11, plaster cast of a right valve (NZGS 5068) from Waikato South Head, Auckland, New Zealand (specimen illustrated by Marwick 1953, pl. 12, fig. 4). The specimen illustrated in fig. 5 is from Tombaugh Cliffs, Alexander Island, and those in figs. 6-10 are from Callisto Cliffs. All specimens × 1.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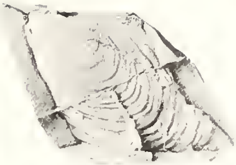
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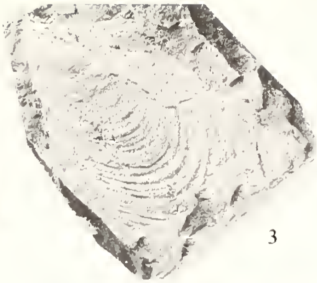
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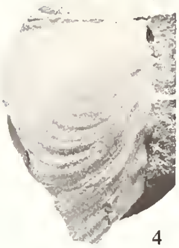
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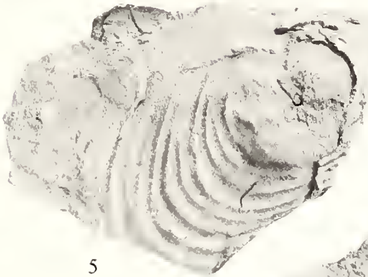
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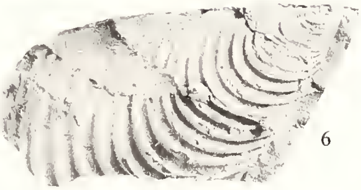
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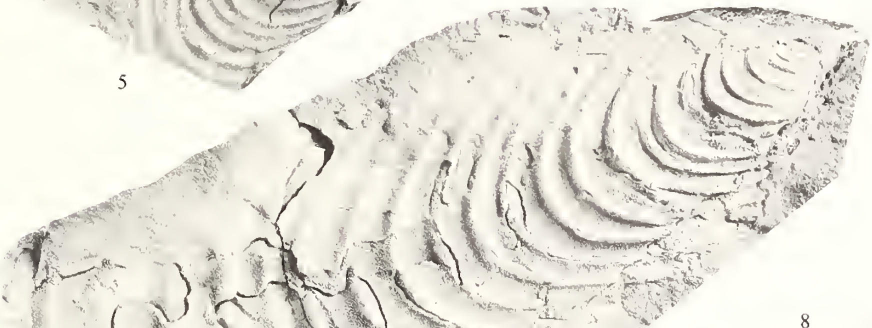
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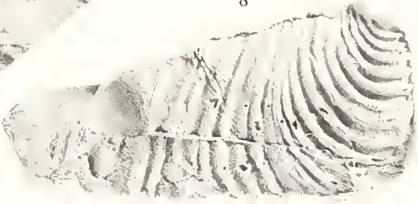
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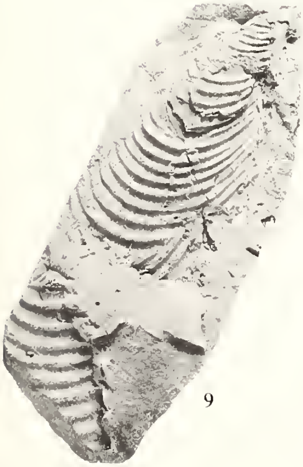
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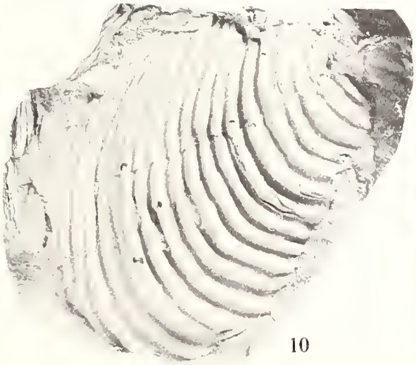
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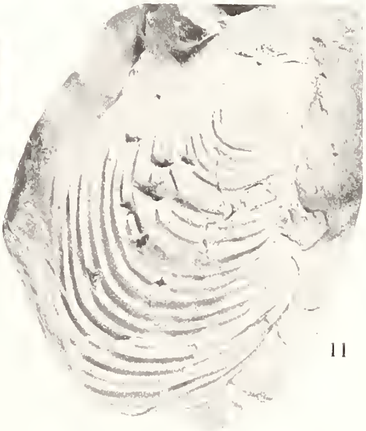
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The stratigraphically oldest right valve, KG.2802.230, has a very similar ornament style to that of KG.2802.32, 132, and 282. The low, narrow ribs are set close together and become finer and even more closely grouped towards the anterior and hinge margins (Pl. 58, fig. 4). However, this specimen seems to be more erect than oblique, and has a larger apical angle (see measurements, below) (Pl. 58, fig. 4). It is also more inflated than any of the left valves. The maximum degree of inflation again occurs in the umbonal region and along the growth axis, and there is a sharp drop from the latter to the anterior margin. Specimen KG.2802.286 (another right valve) is less well preserved, but also appears to be sub-erect in form and to be more inflated along the growth axis. The concentric ribs are very fine but are set slightly further apart than on any of the previous specimens. Some of the flat interspaces in the centre of the valve are up to 1·55 mm in width.

Measurements

Specimen number	L (mm)	W (mm)	W/L	H (mm)	α	β	γ	δ
KG.2802.32 (LV)	35*	18	0·51	14	68°	35°	140°	47°
KG.2802.132 (LV)	43	25	0·58	16	67°	49°	141°	49°
KG.2802.282 (LV)	34	17	0·50	—	60°*	—	—	—
KG.2802.319 (LV)	45*	29*	0·64	19*	72°	—	119°	59°
KG.2802.230 (RV)	50*	30*	0·60	19*	79°	63°	140°*	55°
KG.2802.286 (RV)	40*	26	0·65	19*	59°	48°	136°	46°

Remarks. Retroceramus everesti var. *a* differs from *R. everesti* in its smaller size and finer concentric ornament. It occurs in the Callisto Cliffs section between approximately 92 and 545 m (see later, text-fig. 9).

Retroceramus (*Retroceramus*) *everesti* (Oppel, 1865)

Plate 58, figs. 5–11; Plate 59, figs. 1–11

(?)1833 *Inoceramus*?; Everest, p. 114, pl. 2, fig. 29.
(?)1865 *Inoceramus everesti* Oppel, p. 298.
1865 *Inoceramus hookeri* var. *crenatulinus* Salter; in Salter and Blanford, p. 95, pl. 23, fig. 2.
1913 *Inoceramus everesti* Oppel; Holdhaus, p. 415, pl. 98, figs. 12–14.
1913 *Inoceramus gracilis* Holdhaus, p. 417, pl. 98, fig. 15.
1936 *Inoceramus* cf. *steinmanni* Wilckens; Feruglio, p. 26, pl. 2, figs. 3–11.
1953 *Inoceramus* aff. *everesti* Oppel; Marwick, p. 92, pl. 12, fig. 4.
1960 *Inoceramus* sp. nov. *a* cf. *I. anglicus* Woods; Brunnschweiler, p. 26, pl. 2, figs. 3 and 6, and text-fig. 19.
1960 *Inoceramus* sp. nov. *b* cf. *I. anglicus* Woods; Brunnschweiler, p. 28, pl. 2, fig. 5 and text-fig. 20.
1960 *Inoceramus* sp. nov. *c* aff. *I. neocomiensis* d'Orbigny; Brunnschweiler, p. 29, pl. 2, fig. 4 and text-figs. 21 and 22.
1966 *Inoceramus*; Katz and Watters, p. 336, fig. 7.
1972 *Inoceramus pseudosteinmanni* Thomson and Willey, p. 5, figs. 5*a*–*h*, 6*a*–*c*, and 7*a*.

Material. Eight right valves, fifteen left valves, and numerous fragments from Callisto Cliffs (KG.2802), and two right and two left valves from Tombaugh Cliffs (KG.2803.2, 45, 46, and 112), eastern Alexander Island (text-fig. 5). All the specimens are incomplete internal and external moulds preserved in siltstone: no articulated specimens have yet been collected from Alexander Island.

Description. The best-preserved right valve, KG.2802.384, is an internal mould (covered in places by a thin prismatic shell layer) from the base of the *everesti* zone at Callisto Cliffs (see later, text-fig. 9). In some respects this specimen is slightly atypical of the species as a whole, for it is appreciably larger than any other specimen and has more widely spaced ornament. Although the margins are incomplete, specimen KG.2802.384 can clearly be seen to be narrow and obliquely elongated (Pl. 58, fig. 7). The hingeline appears to have been straight and of moderate length, the anterior margin gently arcuate, and the posterior margin well rounded. A feature of the valve is its very narrow apical angle and small, pointed umbo. The latter is only moderately convex and like the postero-dorsal wing, poorly differentiated from the main body of the valve (Pl. 58, fig. 7). The specimen as a whole is only weakly inflated. The ornament of specimen KG.2802.384 consists of a single set of strong, regularly spaced concentric ribs (Pl. 58, fig. 7). In the umbonal and central regions of the valve these are 1·0–1·5 mm thick and are separated by flat interspaces 2–4 mm in width: ventrally, the ribs thicken to 2·5 mm and the interspaces increase to 5 mm. On the parts of the valve where shell material has been completely removed the ribs have a characteristically rounded cross-section (see also Thomson and Willey 1972, fig. 6). They continue without diminishing in strength across both the wing and umbo.

Specimen KG.2802.655a, from the top of the Callisto Cliffs section, agrees well in general form with KG.2802.384 (Pl. 58, figs. 6, 7), but is much smaller. However, it should be emphasized that, as with so many of these specimens, the margins are incomplete and the original dimensions can only be estimated (see measurements, below). Specimen KG.2802.655a shows the characteristic ornament pattern of simple, clearly defined ribs with symmetrically rounded cross-sections. The ribs are generally 1 mm in width at their summits and are separated by interspaces 1·0–1·5 mm in width: they are thus more closely spaced than on the previous specimen and are more typical of the *everesti* group as a whole.

The two specimens described so far both have umbones that are gently curved in an opisthogyral direction (Pl. 58, figs. 6, 7). This tends to accentuate their obliquity and suggests affinities with *Retroceramus* (see below). However, at least one right valve (KG.2802.544, an internal mould) is much less oblique and in fact has a slightly prosogyrous umbo (Pl. 58, fig. 9). This variation from oblique, opisthogyrous forms to sub-erect, slightly prosogyrous forms seems to be a characteristic feature of the *everesti* group. It occurs in left valves as well as rights (see below), and in a number of specimens from other areas. To some extent it might be explained by post-mortem distortion of what was certainly a thin-shelled species, but it must also reflect original variation in the alignment of the narrow, pointed umbo. There is no consistent stratigraphical separation between the two forms at Callisto Cliffs. Another distinctive feature of specimen KG.2802.544 is its finer ornament. The ribs are still clearly defined and evenly spaced, but their summits are even sharper (Pl. 58, fig. 9). They also show a tendency to fuse and become indistinct on the small postero-dorsal wing.

Specimen KG.2802.439 (an internal mould with traces of shell) is a small, oblique right valve in which the pattern of regular concentric ribbing is considerably disrupted. Clearly defined concentric ribs can be made out over the umbonal and ventral parts of the valve, but in the centre the ribs tend to thicken, fuse, and become uneven in their course. Irregular ribbing such as this is a feature of a number of specimens in the *everesti* group. Two incomplete right valves (KG.2802.462 and 655b) are broader forms with expanded postero-dorsal areas. In neither case are these areas considered to be true wings for they are not clearly separated from the main part of the valve and both still bear strong concentric ribs. On KG.2802.462 the ribs pass on to the area without changing course or diminishing in strength (Pl. 58, fig. 10), but on KG.2802.655b they curve sharply forwards and partially fuse (Pl. 58, fig. 8).

Left valves from near the base of the *everesti* zone at Callisto Cliffs all appear to be small to medium in size and obliquely elongated. Specimen KG.2802.472, a small, narrow internal mould, clearly has an opisthogyral umbonal region which projected slightly above a straight hinge (Pl. 59, fig. 3). The specimen is moderately inflated (with the maximum inflation lying just anterior to the growth axis) and the anterior margin is well demarcated. The ribs are simple, narrow (in the region of 0·5 mm wide at their summits), and regularly spaced. They curve sharply forwards and are set closer together on the postero-dorsal area, but remain individually distinct (Pl. 59, fig. 3). Specimen KG.2802.463, a partially distorted internal mould, is a broader and less inflated left valve (Pl. 59, fig. 9). The hinge and umbonal regions are missing, but the general form of the valve can be judged to have been obliquely elongated. The concentric ribs are particularly clearly and regularly spaced on this specimen. Approximately 0·75 mm in width at their summits, they have the characteristically symmetrically rounded cross-section, and over the central and ventral areas of the valve are separated by shallow interspaces between 2·5 and 3·0 mm in width (Pl. 59, fig. 9). There are traces of a fine prismatic shell layer (less than 0·5 mm thick) along the anterior edge of the valve. Less complete valves, such as KG.2802.417, 418, and 432, are medium sized, slightly to moderately inflated, and obliquely elongated. They all have simple, well-defined concentric ribs, and one of them, KG.2802.417, has an umbo which clearly projects above a short, straight hinge (Pl. 59, fig. 6).

Not all the left valves, however, are obliquely elongated and evenly ribbed. Specimen KG.2802.438, for example, is a broader, more erect form with a considerably expanded postero-dorsal area. Moderately inflated along the growth axis, there are even descents from the central area to the anterior and posterior margins. The ribbing in the central inflated area becomes considerably thickened and confused (in a similar manner to KG.2802.439), and diminishes in prominence towards both the anterior and posterior margins. Much of the extensive postero-dorsal area appears to have been almost smooth.

Perhaps even more striking is the variation shown by two specimens from near the top of the *everesti* zone at Callisto Cliffs. Like the right valve KG.2802.544, both KG.2802.538 and 540 are sub-erect in form and have prosogyrous umbones (Pl. 59, figs. 1, 4). Specimen KG.2802.540, an internal mould of a left valve, is moderately inflated, with the maximum degree of inflation occurring along the growth axis. There are moderately steep descents to the long, straight anterior margin and small postero-dorsal wing. The tip of the umbo and beak are missing, but from the form of the valve they can be judged to have been narrow, pointed, and curved gently forwards (Pl. 59, fig. 4). The concentric ribs are particularly well defined and evenly spaced on this specimen. Symmetrical in cross-section and with narrow, acute summits, they are separated by shallow interspaces varying between 1 mm in width over the umbonal region and 2 mm towards the ventral margin. The ribs tend to die out towards both the anterior margin and the postero-dorsal wing (Pl. 59, fig. 4). Specimen KG.2802.538, an external mould of a left valve, is very similar in size, form, and style of ornament to KG.2802.540 (Pl. 59, fig. 1). The umbonal region and beak of this specimen are also missing, but they can similarly be judged to have been narrow, inflated, and curved gently forwards. Although reduced in strength, concentric ribs can still be distinguished on the postero-dorsal wing of this specimen (Pl. 59, fig. 1).

It should be pointed out here that at least one oblique, opisthogyral left valve (KG.2802.545) (Pl. 59, fig. 2) has been collected from the same stratigraphical level as the prosogyrous specimens KG.2802.538, 540, and 544. Specimen KG.2802.545 (an internal mould with traces of shell material) is characterized by a long, arcuate anterior margin, a long, straight hinge, and an expanded postero-dorsal area (Pl. 59, fig. 2). As in KG.2802.472, the axis of maximum inflation lies anterior to the growth axis and there is a sharp descent to the anterior margin. The umbonal region is incompletely preserved, but can be judged to have been opisthogyrous (Pl. 59, fig. 2). The ornament on this specimen again consists of narrow, regularly arranged ribs which diminish in strength across the postero-dorsal wing.

Another striking trend shown by a number of left valves from the lower levels of the *everesti* zone at Callisto Cliffs is towards the development of coarse, irregular ribs. Specimens showing this trend are incomplete, medium sized internal and external moulds (KG.2802.407, 409–411). They all appear to have been obliquely elongated. On specimens KG.2802.407 and 410 the ribs take the form of broad folds between 2 and 3 mm in width and 2·0 and 2·5 mm in amplitude, and are asymmetric to sub-symmetric in cross-section. They are asymmetric about the growth axis, and are separated by irregular interspaces between 2 and 4 mm in width. Occasionally the ribs anastamose, both in the centre of the valve and towards the margins. Specimen KG.2802.412, a distorted external mould of a left valve, has fine, irregular ribbing over the umbonal region and coarse, irregular ribbing towards the ventral margin.

Numerous fragments found throughout the *everesti* zone at Callisto Cliffs show the characteristic types of *everesti* ornament. There are no clear traces of muscle scars or ligament pits on any of the specimens.

Measurements

Specimen number	L (mm)	W (mm)	W/L	H (mm)	α	β	γ	δ
KG.2802.417 (LV)	76	35	0·46	17	60°*	48°	136°	55°
KG.2802.438 (LV)	81*	55*	0·68	30*	80°	48°	120°	59°
KG.2802.463 (LV)	74	42	0·57	—	51°	44°*	122°	65°*
KG.2802.472 (LV)	55	25	0·45	16*	52°	35°	129°	51°
KG.2802.538 (LV)	55	31	0·56	14*	83°	48°	116°*	60°
KG.2802.540 (LV)	64*	34	0·53	15	84°	43°	106°*	62°*
KG.2802.545 (LV)	49	26	0·53	20	59°*	33°*	123°*	50°
KG.2802.554 (LV)	65°	39	0·60	23*	78°*	52°	126°	64°
KG.2802.384 (RV)	120*	55*	0·46	45*	45°*	37°	155°	28°
KG.2802.439 (RV)	62*	28	0·45	—	41°	36°	—	36°
KG.2802.544 (RV)	50*	26*	0·52	18*	74°	49°	135°	58°
KG.2802.655a (RV)	55*	32*	0·58	18*	59°	39°*	143°	47°
KG.2803.112 (RV)	60*	36*	0·60	25*	63°	48°	122°	52°

Remarks. Specimens collected from the Callisto Cliffs section suggest that members of the *R. everesti* group are typically small to medium sized (for the genus), obliquely elongated (with a few notable exceptions), and weakly to moderately inflated. The group was evidently thin-shelled, for the valve margins seem to have been easily broken and there are only traces of the original shell material. Comparison of similar sized valves suggests that the species was equivalve.

The ornament pattern of narrow, well-defined concentric ribs is particularly diagnostic of the group. The ribs are typically evenly spaced and symmetrically rounded in cross-section, and in the majority of cases are of uniform strength across the whole valve surface. In particular, they are clearly not weakened or excessively crowded over the umbonal region. There are, however, a number of distinct variants within the *everesti* group. The more erect, slightly prosogyrous forms would seem at first sight to be morphologically distinct, but they clearly have a typical *everesti* ornament pattern and cannot be separated on stratigraphical grounds from the more common oblique and opisthogyrous forms. Irregularly ribbed varieties occur at several levels, but never in such a way that they can confidently be separated into either distinct stratigraphical or morphological subgroups. The nature and degree of the variation shown by the Callisto Cliffs specimens suggest that a number of other Southern Hemisphere species can now be accommodated within the *R. everesti* group.

Inoceramus everesti Oppel, a Himalayan species, was first fully described and illustrated by Holdhaus (1913), who had access to a number of specimens from the Middle and Upper Spiti Shales. However, it is apparent that nearly all these specimens are small and incomplete, and the exact form of the original *I. everesti* still remains in some doubt. The largest illustrated specimen (Holdhaus 1913, pl. 98, fig. 12), an internal mould of a left valve, appears to be obliquely elongated, and judging from the form of the concentric ornament, probably had a slightly opisthogyrous umbo. The smaller specimens are much less obviously oblique (Holdhaus 1913, pl. 98, figs. 13 and 14*a–c*) and it would seem that the Himalayan material probably exhibits a range of variation similar to that seen in the Callisto Cliffs specimens. Such a trend is confirmed by examination of a series of undescribed specimens of *I. everesti* (from the Spiti Shales of Niti Pass) housed in the British Museum (Natural History). A small whole specimen (LL.1006) and several single valves (e.g. LL.1004, 1007, and 1011) clearly have erect outlines (e.g. Pl. 59, fig. 5), but specimen LL.1005 is a fragment of a more obliquely elongated left valve (Pl. 59, fig. 8), and LL.1009 may be a slightly obliquely elongated right valve (Pl. 59, fig. 7). Although the latter specimen apparently has a sub-erect outline, there are traces of a postero-dorsal wing and some indications that the valve may have extended for a considerable distance in a ventral direction. Indeed, this specimen is similar to the early stages of the oblique specimens KG.2802.384 and 655a from Callisto Cliffs (cf. Pl. 59, fig. 7 and Pl. 58, figs. 6, 7). *Inoceramus hookeri* Salter 1865 from the Spiti Shales of Niti Pass is probably a distinct species in its own right (within the genus *Retroceramus*) but *I. hookeri* var. *crenatulinus* Salter (*in* Salter and Blanford 1865, pl. 23, fig. 2) belongs within *I.* (= *R.*) *everesti*. It is interesting to note that the single specimen of this variety recorded to date shows a slight variation between the right and left valves, in a manner similar to that of the B.M.(N.H.) specimen (LL.24175) of *R. haasti* from Kowhai Point, south-west Auckland (Pl. 57, figs. 1, 2). Whereas the left valve is very slightly oblique (Pl. 59, fig. 11), the right valve is more erect and has a pointed, slightly prosogyrous umbo (Pl. 59, fig. 10). However, the specimen is incomplete and slightly crushed, and there is no evidence from the other specimens examined of a consistent morphological difference between the valves of *R. everesti* (as is also the case with *R. haasti*). It is also interesting to note that the valves of the specimen of *I. hookeri* var. *crenatulinus* have prominent anterior margins, with that of the left valve being particularly well rounded in cross-section. All the specimens from the Spiti Shales bear the distinctive *everesti* style of ornament.

Oppel (1865) based *I. everesti* on a series of incomplete steinkerns and impressions, one of which had previously been figured by Everest (1833, pl. 2, fig. 29). The latter specimen is likely to become the lectotype, but as the descriptions of it are so brief and the illustration so poor, its identity must be held in some doubt. Everest (1833, p. 114) gives no formal description, and Oppel (1865, p. 298) merely states that it is a broad, irregularly ribbed species. The illustration (Everest 1833, pl. 2, fig. 29) in fact seems to be upside down, so that the true outline is probably rounded-triangular, with a considerably expanded ventral region. There is even a possibility that this specimen could be an *Anopaea*, as *A. stoliczkai* (Holdhaus), a species with a rounded outline and fine, regular concentric ornament, is also known from the Spiti Shales (Crame 1981*b*). It can only be concluded that both the specimen and illustration are totally inadequate for diagnostic purposes and that Everest's (1833) and Oppel's (1865) identifications must be held in some doubt. The earliest reliable guide to the identification of *I. everesti* is that given by Holdhaus (1913), and it would seem prudent to formally regard his illustrated specimens (Holdhaus 1913, pl. 98, figs. 12–14) as plesiotypes of

I. everesti Oppel. *Inoceramus gracilis* Holdhaus (1913, p. 417, pl. 98, figs. 15*a–d*) can now be included within the range of variation established for the *R. everesti* group.

It became apparent at an early stage in this study that the inoceramids from Callisto Cliffs were very close to *I. pseudosteinmanni* Thomson and Willey (1972), a species common in the nearby Tombaugh Cliffs (text-fig. 5). They were obiously similar in size and degree of inflation, and both possess the distinctive *everesti* style of ornament. However, the exact form of *I. pseudosteinmanni* is not immediately obvious. All the specimens described by Thomson and Willey (1972, p. 7, figs. 5*a–h*, 6*a–c*, and 7*a*) are incomplete, with the larger specimens being particularly badly preserved.

The smallest specimens of *I. pseudosteinmanni* apparently have an erect outline (e.g. Thomson and Willey 1972, figs. 5*d* and *f*), but both the holotype (KG.401.520) (fig. 5*b*) and specimen KG.401.521 (fig. 5*h*) are slightly obliquely elongated. The two largest specimens (KG.401.514 and 524) (figs. 5*a* and *e*) have rounded-quadrate outlines, due principally to the development of extensive postero-dorsal areas. Additional material recently collected from Tombaugh Cliffs suggests that at least some of the larger specimens of *I. pseudosteinmanni* may have been obliquely elongated. Specimen KG.2803.112, for instance, an internal mould of a right valve which probably had an original length of at least 60 mm, has an oblique outline and sharply pointed umbo (Pl. 58, fig. 5). There was a comparatively long hingeline and an extensive postero-dorsal area which was only weakly differentiated from the main body of the valve. Specimen KG.2803.46, an external mould of a right valve, also appears to have been medium sized and slightly oblique, whereas KG.2803.45 has a quadrate outline and an extensive postero-dorsal area similar to those of KG.401.514 and 524 (see Thomson and Willey 1972, figs. 5*a*, *e*).

Although smaller and less complete, the specimens from Tombaugh Cliffs do show strong similarities to those from Callisto Cliffs and should now be included in the *R. everesti* group. The smaller specimens agree well with the smaller Spiti specimens (e.g. Holdhaus 1913, pl. 98, figs. 13 and 14; Pl. 59, figs. 5, 7), and forms such as KG.401.515a, 520, and 522 (Thomson and Willey 1972, figs. 5*b*, *c*, and *h*) agree with the less oblique specimens from Callisto Cliffs (e.g. KG.2802.538 and 544; Pl. 58, fig. 9; Pl. 59, fig. 1). There are, in addition, large fragments from Callisto Cliffs (e.g. KG.2802.554 and 555) which have remnants of extensive, flat, postero-dorsal areas very similar to those seen on KG.401.514 and 524 (Thomson and Willey 1972, figs. 5*a*, *e*) and on KG.2803.45.

The South American specimens included by Thomson and Willey (1972, p. 5) in the synonymy of *I. pseudosteinmanni* also fall within the concept of *R. everesti* (see Feruglio 1936, pl. 2, figs. 3–11; Katz and Watters 1966, p. 366, fig. 7). Again, all the specimens are poorly preserved, but they seem to correspond in general form, degree of inflation, and style of ornament with members of the *R. everesti* group. Both Leanza (1967, pp. 147–148) and Thomson and Willey (1972, p. 8) have suggested that two species groups can be distinguished within Feruglio's (1936) material, but

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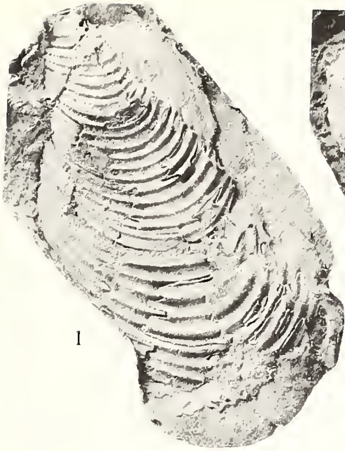
EXPLANATION OF PLATE 59

Figs. 1–11. *Retroceramus* (*Retroceramus*) *everesti* (Oppel). 1, latex peel from an external mould of an erect left valve (KG.2802.538). 2, internal mould of an oblique left valve (KG.2802.545). 3, internal mould of an oblique left valve (KG.2802.472). 4, internal mould of an erect left valve (KG.2802.540). 5, incomplete internal mould of a small left valve (BMNH LL.1006). 6, internal mould of a left valve (KG.2802.417). 7, latex peel from an external mould of a right valve (BMNH LL.1009). 8, incomplete internal mould of a small, oblique left valve (BMNH LL.1005). 9, internal mould of a left valve (KG.2802.463). 10, holotype of *Inoceramus hookeri* var. *crenatulinus* Salter (BMNH LL.1081) viewed from the right side. 11, the same specimen viewed from the left. The specimens illustrated in figs. 1–4, 6, and 9 are from Callisto Cliffs, Alexander Island, and those in figs. 5, 7, 8, 10, and 11 are from the Upper Jurassic Spiti Shales of the Himalayas. All specimens ×1.



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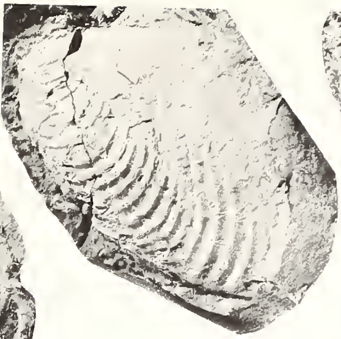

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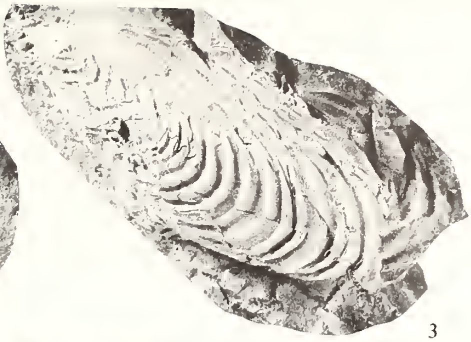

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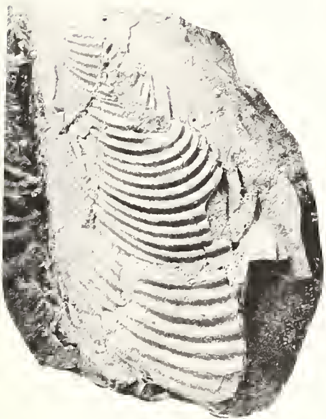

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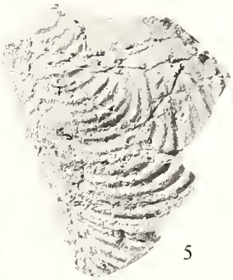

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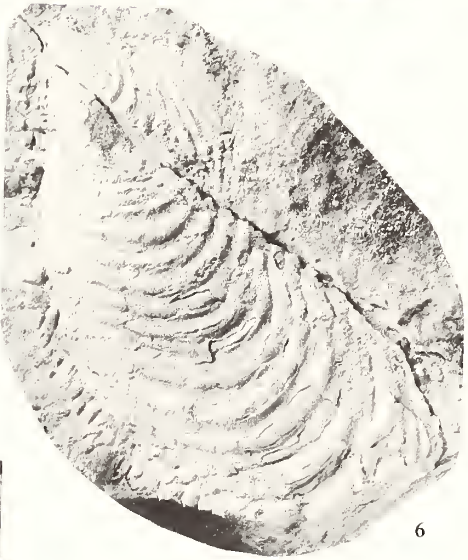

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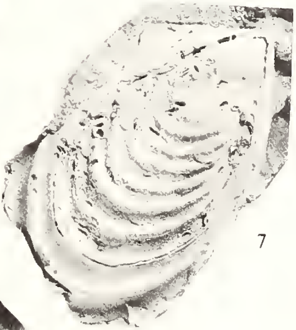

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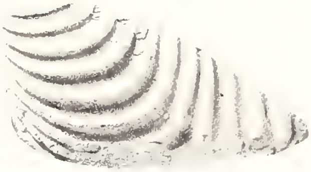

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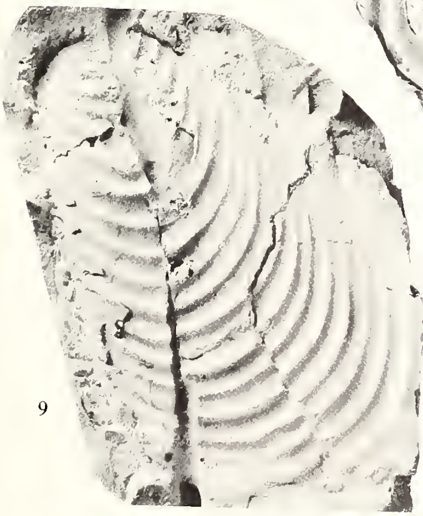

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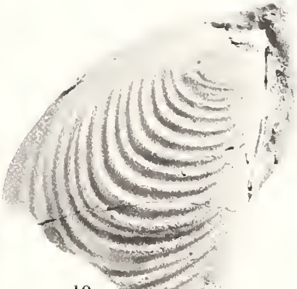

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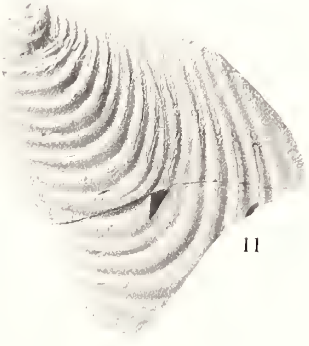


11

CRAME, Inoceramid bivalves

in view of the poor state of preservation, and the wide degree of morphological variation shown by the group as a whole, it would seem better to regard all the specimens as belonging to *R. everesti*. The incomplete, partially distorted valves figured by Feruglio (1936, pl. 2, figs. 3–11) are particularly reminiscent of some of the specimens collected from Tombaugh Cliffs (see Thomson and Willey 1972, figs. 5*a–h*, and Pl. 58, fig. 5).

At least one potential member of the *R. everesti* group has been reported from New Zealand. Marwick (1953, p. 92, pl. 12, fig. 4) (Pl. 58, fig. 11) has illustrated a specimen from South Auckland which seems to be close to the Spiti Shales material, but because it is very weakly inflated he only tentatively identified it as *I.* aff. *everesti*. This specimen is particularly interesting because it is erect in form and has a slightly prosogyrous umbo (Pl. 58, fig. 11). It is similar in outline to specimen KG.2802.544 from Callisto Cliffs (Pl. 58, fig. 9), but is somewhat broader and has a more inflated umbonal region. The narrow, concentric ribs (generally less than 0·5 mm in width) are very similar to those of KG.2802.544. However, it should be pointed out that both the anterior and posterior margins of Marwick's specimen are incomplete, and the umbonal region is worn. No other *everesti*-type material has yet been described from New Zealand, although Marwick (1953, p. 92) mentions that the South Auckland collections include two undescribed juveniles and one fragment. Fleming's (1958, p. 384, fig. 12) specimen of *Inoceramus* n. sp. *A*. ? aff. *everesti* from North Canterbury may well be an *Anopaea* (Crame 1981*b*).

Inoceramus sp. nov. *a* from Dampier Land, Western Australia (Brunnschweiler 1960, pp. 26–27, pl. 2, figs. 3 and 6, and figs. 19*a–c*), seems to be close to *R. everesti*. Small to medium in size and subrhomboidal in outline, it has slightly opisthogyrous umbones and a distinct postero-dorsal wing. The ornament consists of fine, regular concentric ribs with rounded summits. The ribs are separated by interspaces of equivalent width over most of the valve surface, but there are indications of crowding towards the anterior margin and on the postero-dorsal wing. The specimens seem in fact to be more complete versions of those illustrated by Holdhaus (1913, pl. 98, figs. 12–14). The left valves (Brunnschweiler 1960, pl. 2, fig. 6, and fig. 19*c*) are particularly interesting in that they show how a seemingly sub-erect form can sometimes have a distinctly opisthogyrous umbo. Brunnschweiler's (1960, p. 28, fig. 20) *Inoceramus* sp. nov. *b* is similar to *I.* sp. nov. *a*, but is slightly more elongated and has irregular ribbing developed towards the posterior and ventral margins. The specimen is quite clearly oblique, and has a long, straight hinge and distinct postero-dorsal wing. The ribs are regular and well defined, and again there is a strong resemblance to members of the *R. everesti* group. In particular, Brunnschweiler's (1960) specimen illustrated in his figure 20*a* is similar in form to specimens such as KG.2802.472 and 655b from Callisto Cliffs (Pl. 58, fig. 8; Pl. 59, fig. 3).

The only obvious difference between Brunnschweiler's (1960) *I.* sp. nov. *a* and *b* and *R. everesti* is that the concentric ribs of the former two species are set slightly closer together. However, all the specimens illustrated by Brunnschweiler (1960) are incomplete, and it is possible that the interspace width increased slightly towards the ventral margin. It is also apparent that a third species, *I.* sp. nov. *c* (Brunnschweiler 1960, p. 29, pl. 2, fig. 4, and figs. 21 and 22), associated with the previous two, had much coarser and more widely spaced ribs. This species is known only from fragments, but it appears to have been a larger and less obviously oblique form. On the largest fragment (Brunnschweiler 1960, fig. 22*a*), the ribs are up to 2 mm in width at their summits and are separated by interspaces of up to 4 mm. The ribs occasionally anastamose in a manner reminiscent of specimens KG.2802.407–411 from Callisto Cliffs. Just as the latter are thought to be coarser-ribbed varieties of *R. everesti*, so *I.* sp. nov. *c* may be a coarser-ribbed variety of *I.* sp. nov. *a* and *b*. Thus, all three of Brunnschweiler's (1960) new species fall within the current concept of the *R. everesti* group, but it should be pointed out that a number of the original specimens have been lost (see Brunnschweiler 1960, p. 4).

There is some evidence that *R. everesti* may occur in the Sula Islands, Indonesia. Kruizinga (1926) reports that numerous finely ribbed *Inoceramus* fragments are present in the Late Jurassic *Aucella* Marls, and judging from his descriptions (Kruizinga 1926, pp. 21–22), these could well belong to *R. everesti*. When further collections have been made in this area, it may be possible to relate the stratigraphical occurrence of *R.*

everesti to that of other Southern Hemisphere index species (such as *R. galoi*, *R. subhaasti*, and *R. haasti*) in measured sections (see Westermann *et al.* 1978). Thus, in time, the Sula Islands may well become another standard stratotype for Southern Hemisphere Late Jurassic inoceramids. Some of the poorly preserved Jurassic inoceramids from New Caledonia (e.g. Avias 1953, pl. 23, figs. 6–8) may also belong to the *R. everesti* group.

The evidence for reassigning *I. everesti* to the genus *Retroceramus*, although strong, is perhaps slightly less convincing than for either *I. galoi* or *I. haasti*. This is principally because the hinge region of this species is poorly known. The hinge appears to have been long and straight, but is rarely preserved in its entirety. The structure of the ligament area, a crucial feature in generic diagnosis, is also poorly understood. The left valve illustrated by Holdhaus (1913, pl. 98, fig. 12) shows traces of rounded-rectangular ligament pits measuring approximately 2 × 1 mm, and separated by interspaces of equivalent width. A hinge fragment on B.M.(N.H.) specimen LL.1009 shows pits of similar shape and dimensions, separated by clearly defined interspaces up to 1·5 mm in width. Thus, although the pits are somewhat smaller than those normally associated with *Retroceramus*, they are comparatively broad, rounded, and widely spaced. The ligament area as a whole is probably closer to that of *Retroceramus* than *Inoceramus*. In his classification of Jurassic inoceramids, Wandel (1936, p. 467) included *I. everesti* within the *I. haasti* group. All the other members of this group (*I. haasti*, *I. subhaasti*, *I. retrorsus*, and *I. ferniensis*) can now be referred to the genus *Retroceramus*, and it would seem logical to reclassify *I. everesti* here too.

Retroceramus everesti is consistently smaller, less oblique, and more finely ribbed than either *R. haasti* or *R. galoi*. However, the largest form of *R. everesti* from Callisto Cliffs, specimen KG.2802.384 (Pl. 58, fig. 7), does show some similarities to certain varieties of *R. subhaasti*. Wandel (1936, p. 472) himself remarked upon the similarity between *I. subhaasti* var. *denseplicata* (Wandel 1936, pl. 15, fig. 2 and pl. 10, fig. 5*a*) and *I. everesti*, but stated that the latter was characterized by thinner concentric ribs. *Retroceramus subhaasti* is also typically more inflated than *R. everesti*, and has a more strongly projecting umbo (see p. 573). The resemblance is perhaps strongest between KG.2802.384 (Pl. 58, fig. 7) and *R. subhaasti* var. *intermedia* (Wandel 1936, pl. 18, fig. 3*a*). However, this variety clearly has the strongly projecting umbo which is so typical of the *subhaasti* group, and thicker concentric ornament.

Retroceramus everesti also compares well with several Northern Hemisphere species. Small, regularly ribbed forms from Callisto Cliffs (such as KG.2802.472 and 545; Pl. 59, figs. 2, 3) show similarities to species such as *R. rhomboideus* (Voronetz) (Aalenian) from Siberia (Voronetz 1937, pl. 5, figs. 9 and 10, and pl. 10, figs. 2–4), and less regularly ribbed forms (such as KG.2802.438 and 439) to species such as *R. obliquiformis* (McLearn) (Callovian) from Alberta (e.g. McLearn 1924, p. 41, pl. 3, fig. 9). Two Japanese species, *R. utanoensis* (Kobayashi) and *R. ogurai* (Kobayashi) (both Bathonian), are close to *R. everesti*, but are too badly preserved for a detailed comparison to be made (Kobayashi 1926, pl. 11, figs. 1–3).

Available evidence suggests that *R. everesti* is present in both the Middle and Upper Spiti Shales, and thus has a stratigraphical range in the Himalayas of Lower Tithonian–Neocomian (Stevens 1965, p. 149; Helmstaedt 1969). The New Zealand specimen of *I.* aff. *everesti* is of Late Tithonian age (Stevens and Speden 1978, p. 264) and *I. pseudosteinmanni* from Tombaugh Cliffs is Early Berriasian (Thomson and Willey 1972, Table 2). Although there are obvious lithofacies and faunal differences, it would appear that the Callisto Cliffs section can be correlated with the central part of the Ablation Valley section (see later, text-fig. 9). The base of the Callisto Cliffs section is believed to be Late Tithonian in age, and the top Early Berriasian. The top of the Callisto Cliffs section correlates with the base of the Tombaugh Cliffs section (see later, text-fig. 9), and the range of *R. everesti* in Alexander Island can be established as Late Tithonian–Early Berriasian. Of the species synonymized within *I. pseudosteinmanni*, *Inoceramus* (Katz and Watters 1966, p. 336) comes from the Yahgan Formation of Patagonia, which spans the Jurassic–Cretaceous boundary, and *I.* cf. *steinmanni* Wilckens has a probable origin in sedimentary rocks of Upper Tithonian–Berriasian age (Feruglio 1936; Leanza 1967). The three new inoceramid species described by Brunnschweiler (1960) from Dampier Land, Western Australia, were also obtained from a thick sequence of transitional Jurassic–Cretaceous deposits. The Leveque Sandstone, in which the three species were found, is judged to be Early Neocomian, but it is possible that it may be partly Late Tithonian in age too (see discussion section, below).

It may be concluded that *R. everesti* is a small- to medium-sized species characteristic of Southern Hemisphere Late Tithonian–Early Berriasian strata. The valves are typically obliquely elongated, weakly to moderately inflated, and bear fine, regular concentric ribs. There are, however, a number of distinct variations on this basic theme: some forms clearly have more erect outlines, and others developed irregular or coarse ornament. The features shown by *R. everesti* are in fact such as to suggest that this species occupies an intermediate position between *Retroceramus* and *Inoceramus*.

In particular, the following features suggest an evolutionary trend away from the typical *Retroceramus* morphology towards that of *Inoceramus*:

(i) The specimens are generally smaller and less obviously oblique than many species of *Retroceramus*.
(ii) The shell is thinner than in many *Retroceramus* species, and the hinge and ligament areas are apparently reduced in thickness.
(iii) The ligament pits are probably transitional in form between those typical of *Retroceramus* and those typical of *Inoceramus*.
(iv) The ornament is finer than in most species of *Retroceramus*.

An intermediate position between *Retroceramus* and *Inoceramus* is further suggested by the consistent stratigraphical occurrence of the species at the Jurassic–Cretaceous boundary. *Retroceramus* is essentially restricted to the Jurassic, and *R. everesti* must be a member of one of the latest stocks of this genus. Data on Early Cretaceous inoceramids are sparse, but it would appear that nearly all the species so far described can be referred to *Inoceramus*.

Retroceramus (*Retroceramus*) sp. nov. 1

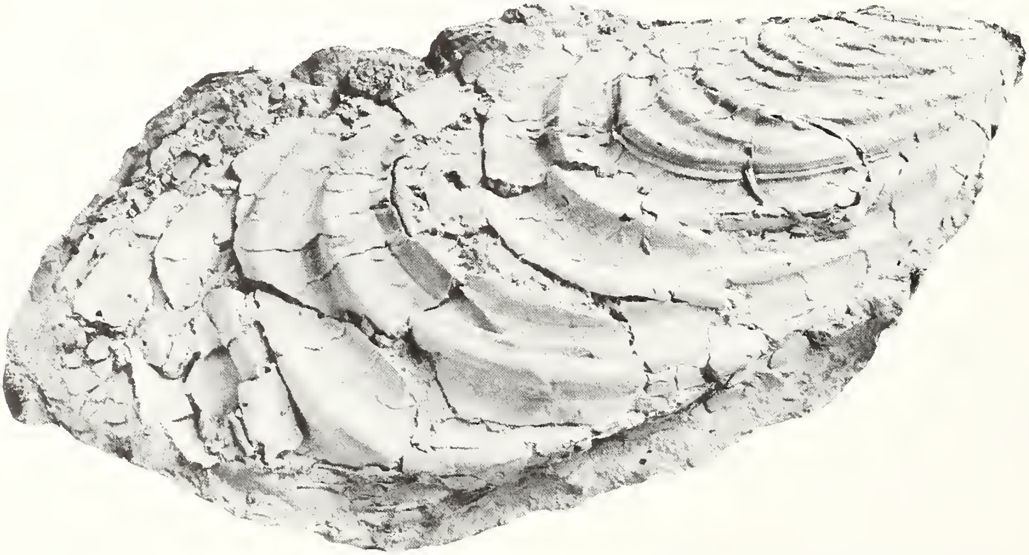
Text-fig. 6

(?)1953 *Inoceramus* sp. 'G' Sornay; *in* Routhier, p. 56, pl. 2, fig. 7.
1972 *Inoceramus* aff. *subhaasti* Wandel; Thomson and Willey, p. 3, fig. 3.

Material. One large but incomplete external mould (KG.701.76) from the same locality in Ablation Valley as the specimen of *R. haasti* (KG.701.74). The specimen is preserved in fine-grained, tuffaceous sandstone.

Measurements. KG.701.76 (RV): L 150* mm. W 62 mm, W/L 0·41, α 53°*, β 45°*, δ 34°*.

Remarks. This is a distinctive, narrow, obliquely elongated right valve that cannot be readily matched with any previously described species. In form and outline it resembles *R. galoi*, but the



TEXT-FIG. 6. *Retroceramus* (*Retroceramus*) sp. nov. 1. Latex peel from an external mould of a right valve (KG.701.76) from the south side of Ablation Valley, Alexander Island; ×1.

ribbing is altogether too coarse and widely spaced for it to be considered a member of that species (Thomson and Willey 1972, p. 3). There are obvious resemblances to the more oblique forms of *R. haasti* (e.g. Wandel 1936, text-fig. 4 and pl. 20, fig. 1), but the valve is consistently narrower than a typical *haasti*, showing no tendency towards marked postero-ventral expansion (text-fig. 6). The style of ornament differs from that of *R. haasti* in that there are fine secondary ribs intercalated between the prominent primaries. There is also some tendency for the primaries to fuse close to the ventral margin (especially in the umbonal region, see Thomson and Willey 1972, fig. 3 and text-fig. 6). The specimen resembles some of the poorly preserved Late Jurassic inoceramids from New Caledonia, and Thomson and Willey (1972, p. 3) compared it directly to *I.* sp. 'G' Sornay (*in* Routhier 1953, pl. 2, fig. 7). However, taking into account the poor state of preservation of this specimen and the fact that the hinge is missing, it can only be tentatively included in *R.* sp. nov. 1.

Routhier (1953, p. 56, pl. 2, fig. 9) illustrated a second obliquely elongated, coarsely ribbed inoceramid as *I.* sp. cf. *subhaasti*. This specimen, although of similar dimensions to KG.701.76, has thicker concentric ribs that have acute summits and distinctly triangular cross-sections. These ribs are set close together and continue almost undiminished in strength across the umbo. Such a style of ornament is in fact closer to that seen in certain Middle Jurassic Boreal species of *Retroceramus*, such as *R.* (*R.*) *porrectus* Eichwald (e.g. Koshelkina 1963, pl. 6, fig. 1) or *R.* (*R.*) *ferniensis* (Warren) (e.g. Warren 1932, pl. 2, fig. 1), than to any previously described Late Jurassic species. *Inoceramus* sp. A (Avias 1953, p. 169, pl. 23, figs. 1 and 2) from New Caledonia also appears to be medium sized, obliquely elongated and coarsely ribbed, but the specimens are too poorly preserved to enable any positive identifications to be made. *Inoceramus* sp. B (Avias 1953, pl. 23, fig. 3), apart from having a slightly more erect form, seems to be close to Routhier's (1953) *I.* cf. *subhaasti*.

From its association with *R. haasti* in Ablation Valley, *R.* sp. nov. 1 is judged to have an age range of Middle Kimmeridgian–Tithonian.

Retroceramus (*Retroceramus*) sp. nov. 2

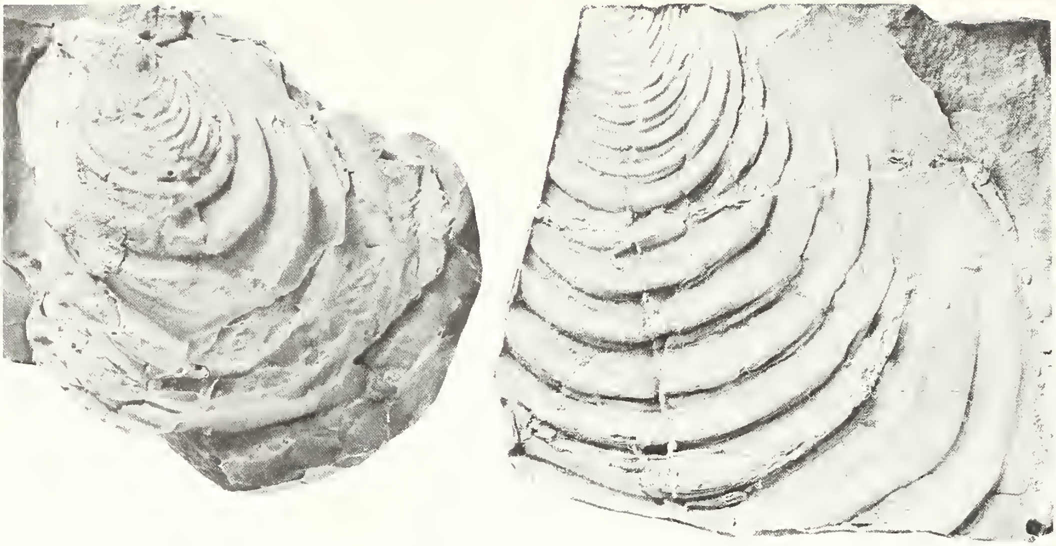
Text-fig. 7*a*, *b*

1972 *Inoceramus* sp.; Thomson, p. 97, fig. 3*c*.

Material. One incomplete external mould (T.535,10) from Adelaide Island (text-fig. 1). The specimen is preserved in a pale, grey-green tuff, and comes from a marine horizon at the base of a 3000 m volcanic sequence.

Description. This is a medium sized, rounded to sub-quadrate left valve. Although the anterior and ventral margins are missing, it can be judged to be broader and more erect than any of the previously described species (text-fig. 7*b*). It is only feebly inflated, but in all probability has been partially crushed. One of the most distinctive features of the specimen is its concentric ornament, for the ribs are markedly asymmetric in cross-section. Between 5 and 8 mm in width in the centre of the valve, they have long, gently descending dorsal (or umbonal) slopes, and short, nearly vertical, ventral slopes (text-fig. 7*b*). The ribs are clearly defined and regular in their course in the centre of the valve, but are much thinner (1·0–1·5 mm in width) over the umbo. They disappear completely in the postero-dorsal area where there is an ill-defined, almost smooth wing (text-fig. 7*b*).

Specimen T.535.10 compares well with an undescribed specimen in the New Zealand Geological Survey collections (NZGS 9932, text-fig. 7*a*) identified as *I.* aff. *subhaasti* Wandel. This specimen is an almost complete small- to medium-sized left valve. It too has a rounded-quadrate outline, but is considerably more inflated than the Adelaide Island specimen. A notable feature is that the anterior margin is broad and drops steeply to the plane of commissure (text-fig. 7*a*). The umbo is strongly prosogyrous and projects above a long, straight hingeline (text-fig. 7*a*). The ornament consists of prominent concentric ribs that again have the characteristic step-like profiles in cross-section. They are of similar dimensions to those of T.535.10, and also become noticeably finer over the umbo. The ribs die out on the indistinctly recessed postero-dorsal wing (text-fig. 7*a*).



TEXT-FIG. 7. *Retroceramus* (*Retroceramus*) sp. nov. 2. *a* (left), plaster cast of a left valve in the New Zealand Geological Survey collections (NZGS 9932) identified as *Inoceramus* aff. *subhaasti* Wandel; collected from Old Kihi Road, Hauturu, Kawhia. *b* (right), latex peel of an external mould of a left valve (T.535.10) from the south-western corner of the Mount Bouvier massif, Adelaide Island. Both specimens ×1.

Measurements. T.535.10 (LV): L 110* mm, W 73* mm, W/L 0·66, H 40* mm, α 80°*, β 55°*, γ 120°, δ 67°*. NZGS 9932 (LV): L 67 mm, W 54* mm, W/L 0·81, H 30* mm, α 81°, β 55°, γ 120°*, δ 66°.

Remarks. The two specimens described above appear to belong to a new species of *Retroceramus*. That a member of this genus could have a rounded-quadrate outline is not altogether unreasonable, for several Boreal species have similar growth forms. *Retroceramus* (*Retroceramus*) *eximius* Eichwald, for example, an Aalenian species, has a distinctly rounded-quadrate outline, as well as strongly projecting umbones (e.g. Eichwald 1871, pl. 18, figs. 1 and 2, and pl. 19, figs. 3 and 4), and *R.* (*R.*) *polaris* Koshelkina, a Bathonian species, has a rounded outline, coarse ribs over the main part of the valve, and finer ribs over the umbo (e.g. Koshelkina 1962, pl. 9, fig. 5). It is also apparent that in cross-section the prominent anterior margin of *R.* sp. nov. 2 was wedge-shaped rather than a flat shelf (text-fig. 7*a*), and thus the species would almost certainly have been functionally endobyssate.

Specimen NZGS 9932 from New Zealand is probably one of the specimens identified by J. B. Waterhouse (*in* Fleming and Kear 1960, p. 43) as *I.* cf. *subhaasti*. These specimens (none have been formally described or illustrated) subsequently assumed considerable importance in New Zealand Jurassic biostratigraphy, for they seemed to occupy intermediate morphological and stratigraphical positions between the well-known species *galoi* and *haasti* (Stevens 1965, 1968; Speden 1970). However, in both form and style of ornament, specimen NZGS 9932 clearly differs from all members of the *R. subhaasti* group and should not now be associated with that species. There may well be transitional forms between *R. galoi* and *R. haasti* in New Zealand (see, e.g., Stevens 1968, p. 62), but it has yet to be demonstrated that any of them belong to *R. subhaasti*. The postulated *galoi–subhaasti–haasti* lineage in New Zealand is currently in need of detailed revision (Spörli and Grant-Mackie 1976, p. 28).

Associated fossils from Adelaide Island (locality T535) have Late Jurassic affinities, but are undiagnostic as to stage level (Thomson 1972, p. 100). Specimen NZGS 9932 is dated as Ohauan in New Zealand, and this stage is generally taken to be equivalent to the Middle Kimmeridgian (e.g. Speden 1970, p. 828). However, as mentioned previously, there is some possibility that the Ohauan stage may be as late as Late Tithonian.

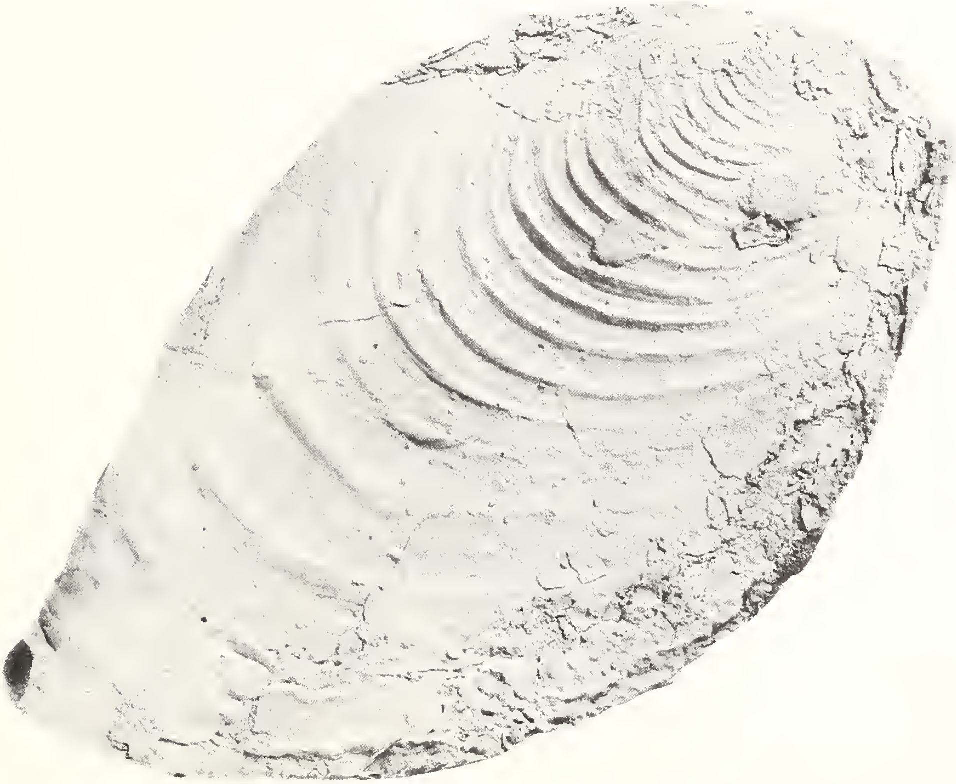
Retroceramus (*Retroceramus*) sp. nov. (?)

Text-fig. 8

Material. Two incomplete single valves (D.3825.6 and D.4329.14) from Longing Gap, Trinity Peninsula (text-fig. 1). The specimens are preserved in a grey, finely bedded siltstone.

Description. These are two flattened and partially distorted external moulds. The margins of both specimens are incomplete, but their general form and regular ornament suggest affinities to *Retroceramus*. The largest specimen (D.3825.1) has a rounded-oval outline and can be judged to have been obliquely elongated (text-fig. 8). The anterior margin appears to have been long and arcuate, and the ventral and posterior margins well rounded. The umbonal region is not clearly differentiated from the main body of the valve but there are remnants of a long, straight hinge and narrow postero-dorsal wing (text-fig. 8). The concentric ribs are closely and evenly spaced over the umbonal region. They have symmetrical profiles and rise to acute summits less than 0·5 mm in width. The ribs become lower, more rounded, and more widely spaced towards the ventral margin (text-fig. 8). The largest of these later ribs are up to 4 mm in width and are separated by interspaces 11 mm in width. In the region of the postero-dorsal wing the ribs sweep sharply forwards and become much finer. There are faint traces of very thin secondary ribs on some of the primaries.

The second specimen (D.4329.14) also appears to have been obliquely elongated. Judging from the course of the concentric ribs, the anterior margin was long and arcuate, the ventral margin well rounded and the



TEXT-FIG. 8. *Retroceramus* (*Retroceramus*) sp. nov. (?). Latex peel from an external mould of a right valve (D.3825.6) from Longing Gap, Trinity Peninsula; × 1.

posterior margin gently rounded. The concentric ribs are again narrow and sharply defined over the umbonal region, but broader and more widely spaced towards the ventral margin. They also become much finer and crowded on the indistinctly recessed postero-dorsal wing.

Measurements. D.3825.6 (RV): L 155* mm, W 95* mm, W/L 0·61, α 82°, δ 47°. D.4329.14 (LV): L 63* mm, W 37 mm, W/L 0·59, H 33* mm, α 58°, γ 132°, δ 52°.

Remarks. There are obvious resemblances between these two specimens and members of the *R. haasti* group (see, e.g., Wandel 1936, text-figs. 4 and 5, pl. 19, fig. 1 and pl. 20, figs. 1 and 2; Pl. 57, figs. 1-4). The obliquely elongated outline and prominent concentric ornament, together with the presence of a distinct postero-dorsal wing and finer-ribbed umbo, all suggest allegiance to this species. However, the valves of *R. haasti* are typically moderately to strongly inflated and have much stronger, projecting concentric ribs. It should also be re-emphasized that the margins of these specimens are incomplete, and their true form is unknown. There is, again, some resemblance to certain elongated, coarsely ribbed Middle Jurassic species (such as *R.* (*R.*) *elongatus* and *R.* (*R.*) *borealis*), but no definite links can be established with either of these forms.

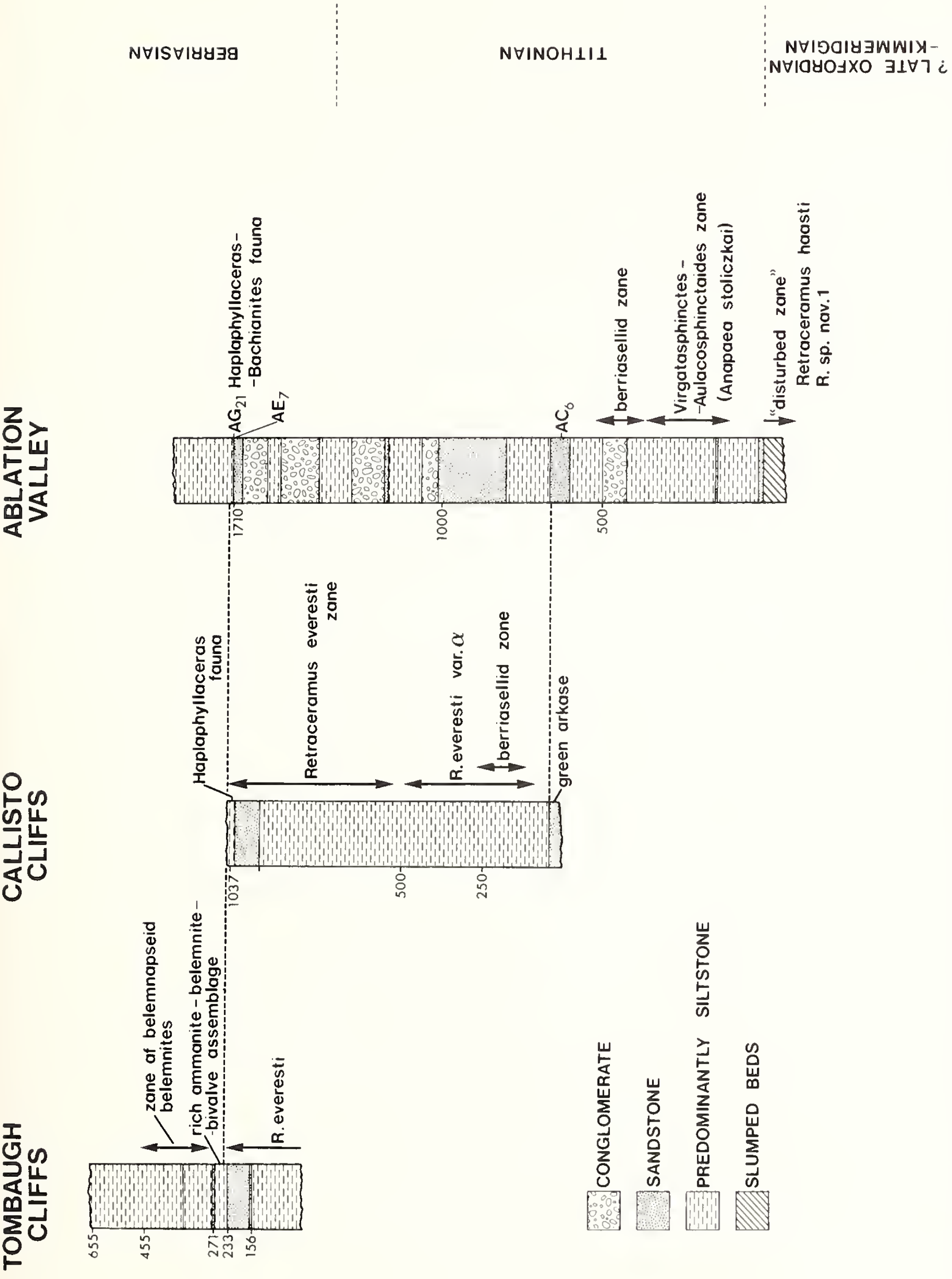
It can be tentatively concluded that these specimens belong to *Retroceramus* and have probable Late Jurassic affinities. Loose perisphinctid ammonites collected from the same general area have a probable Oxfordian or Kimmeridgian age (Aitkenhead 1975, p. 11; Bibby 1966, p. 8).

STRATIGRAPHICAL DISCUSSION

Correlation of the Ablation Valley, Callisto Cliffs, and Tombaugh Cliffs sections, eastern Alexander Island

The Fossil Bluff Formation crops out in a narrow strip along the eastern margin of Alexander Island (text-figs. 1 and 5). It is bounded to the west by a major fault and to the east by George VI Sound. The topography of the area of outcrop consists of a series of isolated massifs separated by west-east trending glaciers draining into George VI Sound (text-fig. 5). There is a predominant south-westerly dip throughout the formation and in general the massifs become progressively younger from north to south. Late Jurassic strata are exposed at Belemnite Point and Ablation Point, and Aptian-Albian strata in the Waitabit Cliffs-Keystone Cliffs area (text-fig. 5) (Taylor *et al.* 1979). However, the stratigraphy is complicated by tectonic disturbances and pronounced lateral facies changes, and correlation between adjacent massifs is by no means straightforward. The formation is composed predominantly of clastic sediments (siltstones, fine to coarse sandstones, and conglomerates), and has an estimated total thickness of approximately 4000 m (Taylor *et al.* 1979; Thomson, in press).

Recent investigations (Elliott 1974) have shown that an extensive sedimentary sequence is exposed within the Ablation Valley massif (text-figs. 5 and 9). The beds in this region dip more westwards than south-westwards (although there are variations due to local folding and faulting) and Elliott (1974) has indicated that a total thickness of more than 2000 m of strata is exposed (ranging in age from ? Upper Oxfordian-Kimmeridgian to Berriasian). The oldest beds in the sequence, comprising the so-called 'disturbed zone', contain spectacular large-scale slump structures (see Bell 1975). The zone probably has a maximum thickness of about 350 m in the Ablation Point region but no accurate stratigraphical measurements have yet been made of it. Although no *in situ* fossils have been collected from it either, there are a number of loose specimens from associated screes. One incomplete perisphinctid ammonite has been identified as *Perisphinctes* (*Orthosphinctes*) cf. *transatlanticus* Steinmann (Howarth 1958), and there are four species of belemnite; *Belemnopsis* cf. *tanganensis* (Futterer), *B.* cf. *alfurica* (Boehm), *B.* cf. *gerardi* (Oppel), and *B.* cf. *keari* Stevens (Willey 1973). Collectively, these five species have been taken to indicate an Upper Oxfordian-Kimmeridgian age (e.g. Elliott 1974; Taylor *et al.* 1979; Thomson 1979). Two loose inoceramids, *R.* (*R.*) *haasti* and *R.* (*R.*) sp. nov. 1, have also been collected from the disturbed zone and the former of these suggests a probable Middle Kimmeridgian-Tithonian age. The most likely age for



TEXT-FIG. 9. Stratigraphical correlations between Ablation Valley, Callisto Cliffs and Tombaugh Cliffs, Alexander Island (see text-fig. 5). Collectively, these three sections comprise approximately the lower half of the Fossil Bluff Formation. The values to the left of each column indicate height in metres above the base of the section and those to the right of the Ablation Valley column are station numbers used by Elliott (1974). Stage boundaries are only approximate.

the disturbed zone would thus seem to be Kimmeridgian, but it is possible that it both ranges down into the Oxfordian and up into the Tithonian.

Between 125 and 400 m in the Ablation Valley section there is a sequence of fossiliferous shales characterized by a distinctive Tithonian ammonite fauna. Species of *Virgatosphinctes* and *Aulacosphinctoides* are particularly common (text-fig. 9), and many of these have strong Lower Tithonian affinities. However, certain Late Tithonian elements are also present in the fauna, and it is probably best to regard this zone as undifferentiated Tithonian in age (Thomson 1979, p. 31). Directly above, between approximately 400 and 500 m, there is another distinctive ammonite zone, characterized by berriasellids (text-fig. 9). Species of *Blandfordiceras* predominate, and the zone as a whole can best be dated as Late Tithonian (Thomson 1979, p. 31). Above this level the next distinctive faunal horizon does not occur until approximately the 1710 m level (text-fig. 9), where a *Bochianites–Haplophylloceras* ammonite assemblage and *Belemnopsis* belemnite assemblage represent the earliest Cretaceous (Berriasian) fauna (Thomson 1979, p. 31; Willey 1973, p. 55). The topmost levels of the section are entirely contained within the Berriasian (Elliott 1974).

Strata exposed in the Callisto Cliffs massif (text-figs. 5 and 9) can be correlated with the central portions of the Ablation Valley section. There is no indication of the *Virgatosphinctes–Aulacosphinctoides* assemblage in the Callisto Cliffs section but there is a distinctive berriasellid fauna between 117 and 264 m (text-fig. 9). Most of the specimens can probably be referred to *Blandfordiceras* and there would appear to be good agreement at the specific level with the Ablation Valley berriasellid zone (Thomson 1979). Unfortunately, there are no other distinctive ammonite horizons in the section. There is one specimen from the 317 m level which can possibly be referred to a Late Tithonian spiticeratid genus, but nearly all the other specimens found are undiagnostic phylloceratids. However, near the top of the section, at a level corresponding approximately to the distinctive *Bochianites–Haplophylloceras* horizon in Ablation Valley (text-fig. 9), there are a number of specimens that can be referred to *Haplophylloceras*: the topmost beds at Callisto Cliffs seem in fact to be equivalent to those at the 1710 m level in Ablation Valley (text-fig. 9). Here, in a sequence of bioturbated, silty shales, there is a very distinctive fauna which includes *Haplophylloceras* sp., *Belemnopsis alexandri* Willey, *Retroceramus everesti*, plant fragments and species of the bivalves *Grammatodon*, *Myophorella*, *Pinna*, and *Panopea*. This fauna is very similar to that found in beds AE_7 and AG_{21} at Ablation Valley (except that *R. everesti* is apparently absent here—Elliott 1974, p. 95), and the 1037 m level at Callisto Cliffs can be directly correlated with the 1710 m level in the Ablation Valley section (text-fig. 9).

The basal 40 m of the Callisto Cliffs section is composed of a distinctive green arkose that contains small conglomerate lenses, belemnite fragments, and large numbers of tiny indeterminate bivalve moulds. This arkose correlates well with a zone of very similar lithology in the lower levels of the Ablation Valley section (bed AC_6 of Elliott 1974, fig. 5). In fact, the thickness of strata between beds AC_6 and AG_{21} at Ablation Valley is almost exactly equivalent to that exposed in the Callisto Cliffs section (text-fig. 9). Nevertheless, it should be pointed out that although the respective sections compare well in thickness, they differ somewhat in lithology; none of the four prominent conglomerate beds present in the Ablation Valley section occurs at Callisto Cliffs (text-fig. 9 and Elliott 1974, fig. 5). In the latter area the strata are predominantly siltstones with intercalated sandstone bands. The conglomerates themselves vary considerably in thickness in the Ablation Valley massif and it is apparent that they pass laterally into sandstones and siltstones. Belemnites tentatively identified from Callisto Cliffs include *Belemnopsis gladiatoris* Willey, *B.* aff. *uhligi* Stevens, *Hibolithes antarctica* Willey, *H. belligerundi* Willey, and *H.* sp. nov. (?): the large, distinctive species, *B. alexandri*, occurs only in the topmost level (1037 m, text-fig. 9). *Retroceramus* (*Retroceramus*) *everesti* var. *a* is present between 92 and 545 m, and *R.* (*R.*) *everesti* between 623 m and the top of the section.

From all the foregoing palaeontological evidence, it can be concluded that the lower levels of the Callisto Cliffs section are Late Tithonian in age and the topmost levels Berriasian. The exact position of the Jurassic–Cretaceous boundary has yet to be determined, but it probably lies in the upper 200–300 m of the section, within the *R.* (*R.*) *everesti* zone (text-fig. 9).

Using both lithological and faunal criteria, it is possible to correlate the top of the Callisto Cliffs section with the lower levels of Tombaugh Cliffs (text-figs. 5 and 9). A prominent band of massive sandstones between 935 and 1014 m at the former correlates well with a similar zone between 160 and 233 m at the latter (text-fig. 9). Few fossils occur in either zone, but both exhibit similar lithologies. Massively bedded sandstones predominate, separated by thinner, finely laminated beds of sandstone and siltstone, and irregular seams of conglomerate. The massive sandstones contain conspicuous cannonball concretions and show traces of shallow cross-bedding. The 156 m of siltstones beneath these sandstones at Tombaugh Cliffs (text-fig. 9) have yielded several types of bivalve (including *R. everesti*), the ammonites *Substreblites*, *Phylloceras*, and *Sarasinella*, and the belemnites *H. antarctica* and *H.* sp. nov. (?) (Willey 1972, 1973; Thomson 1974). Above the massive sandstone zone there is a 38-m siltstone zone (text-fig. 9) containing a prolific invertebrate fauna. Ammonites present include *Phyllopachyceras* (?), *Neocosmoceras*, *Himalayites*, and an indeterminate berriasellid, and there are at least four species of the belemnite genus *Hibolithes*. *Retroceramus everesti* is common, and there are also representatives of the genera *Pinna*, *Myophorella*, *Panopea*, *Grammatodon*, and (?) *Lucina*. Although the correspondence in terms of species composition is not exact, it would appear that this sequence of fossiliferous beds can be correlated in general terms with similar prolific horizons at the 1037 m level at Callisto Cliffs and 1710 m level at Ablation Valley (text-fig. 9) (see also Taylor *et al.* 1979, p. 17). There is no evidence of the ammonites *Haplophylloceras* and *Bochianites*, or of belemnopseid belemnites in this zone (i.e. between 233 and 271 m, text-fig. 9), but the latter do occur only a short distance higher up in the sequence. *Belemnopsis alexandri*, *B. gladiatoris*, and *B.* aff. *uhligi* have all been recorded between 274 and 455 m (Willey 1972). *Retroceramus everesti* is absent above the 246 m level at Tombaugh Cliffs (text-fig. 9).

Correlation of these three sections enables a sequence of inoceramid species to be established for the lower levels of the Fossil Bluff Formation (text-fig. 9). With the addition of two further species, *R. subhaasti* and *R. galoi*, a comprehensive scheme of Late Jurassic inoceramid biozones can be erected (Table 2) that facilitates stratigraphical correlations on both local and regional scales. *Retroceramus subhaasti* is placed beneath *R. haasti* in accordance with its occurrences in Misol and the Sula Islands (Indonesia), and *R. galoi* beneath *R. haasti* in accordance with its occurrences in the Sula Islands and New Zealand. To date, no clear indication has been given as to whether *R. subhaasti* and *R. galoi* can be stratigraphically separated, and thus they are grouped together in Table 2. *Anopaea stoliczkai* (Holdhaus) occurs at Belemnite Point (text-fig. 5) in strata equivalent to the *Virgatosphinctes–Aulacosphinctoides* zone at Ablation Point (Crame 1981*b*). It thus occurs stratigraphically above *R. haasti* but beneath *R. everesti* (text-fig. 9 and Table 2).

TABLE 2. A sequence of Southern Hemisphere Late Jurassic inoceramid biozones and their stratigraphical ranges. The ranges for the upper three species are based on their occurrences in the lower Fossil Bluff Formation of Alexander Island and the lower two species on their occurrences in Antarctica, New Zealand, and Indonesia. N.B. In this table and text-fig. 10 the broadest possible stratigraphical ranges have been given to *Retroceramus galoi*, *R. subhaasti*, and *R. haasti*. It is likely that in the future these ranges will be considerably refined

Inoceramid biozones	Stratigraphical range
Retroceramus everesti (Oppel)	Late Tithonian–Early Berriasian
Anopaea stoliczkai (Holdhaus)	Tithonian
Retroceramus haasti (Hochstetter)	Kimmeridgian–Early Tithonian
Retroceramus subhaasti (Wandel) *Retroceramus galoi* (Boehm)	? Early Kimmeridgian–Tithonian

Stratigraphical correlation within the Antarctic Peninsula

The use of inoceramids in correlation is discussed for the following occurrences.

1. The specimens of *R.* sp. cf. *subhaasti* from Carse Point on the west coast of the Antarctic Peninsula (text-fig. 1) come from a thin (75 m) marine sequence exposed at the base of a thick (900 m) series of tuffs and lavas belonging to the Antarctic Peninsula Volcanic Group. Associated ammonites (principally species of *Kossmatia*) indicate a Middle to Upper Tithonian age for the sedimentary rocks, but belemnites and bivalves suggest a broader Kimmeridgian to Upper Tithonian age range (Thomson 1975). The presence of *R.* sp. cf. *subhaasti* suggests that the marine beds at Carse Point may correlate with a level below that of the disturbed zone at Ablation Valley (text-fig. 9 and Table 2), and this may well explain why *Kossmatia* has not so far been recorded from Alexander Island. It is interesting to note that in the Late Jurassic deposits of New Zealand a *Kossmatia* zone occurs stratigraphically some distance beneath a Tithonian *Aulacosphinctoides* zone (e.g. Stevens 1965, fig. 13; Stevens and Speden 1978, table 2), although it should be emphasized that the exact status of some of the New Zealand *Kossmatia* specimens is uncertain (Verma and Westermann 1973; Thomson 1975, p. 41).

2. Marine fossils have also been recorded from sedimentary volcanic rocks within the Antarctic Peninsula Volcanic Group of Adelaide Island (text-fig. 1). Although the stratigraphy of the latter has yet to be fully resolved, the fossils (from locality T.535 at the south-west corner of the Mt. Bouvier massif) probably occur at a level close to the base of a 3000 m sequence of lavas and volcaniclastic rocks (Dewar 1970; Thomson 1972). Most of the specimens within the assemblage are poorly preserved, but at least one ammonite and two bivalves have general Jurassic affinities (Thomson 1972). The two best preserved specimens are the bivalves *Retroceramus* sp. nov. 2 and *R.* sp. juv.: the latter is undiagnostic, but the former also occurs in New Zealand in the Middle Kimmeridgian Ohauan stage (p. 586). Thus, it is likely that the Mt. Bouvier assemblage can be correlated with either the *R. haasti* or *R. subhaasti* zones of the standardized succession (Table 2). The existence of perhaps as much as 3000 m of volcanic rocks above a Late Jurassic marine horizon suggests that the Antarctic Peninsula Volcanic Group on Adelaide Island ranges well into the Cretaceous (see also Taylor *et al.* 1979; Jefferson 1980).

3. Fossiliferous sedimentary rocks also occur in close association with the Antarctic Peninsula Volcanic Group along parts of the east coast of Trinity Peninsula (Aitkenhead 1975). At Longing Gap (text-fig. 1) a 107 m sequence of siltstones and shales has been recorded as the probable source area for a series of loose ammonites and bivalves (Standring 1953). The exact stratigraphical relationship of these sedimentary rocks to the volcanic rocks exposed further inland is uncertain, but the occurrence of several tuffaceous bands in the sequence suggests that their formation was at least in part coeval with the volcanism. The fossils from Longing Gap are all poorly preserved: they occur as moulds in a fissile siltstone and all have been crushed and partially distorted. The two best preserved bivalves can be tentatively assigned to a new *Retroceramus* species (*R.* sp. nov. ?) with possible Late Jurassic affinities (p. 587), and there are perisphinctid ammonites which can be compared to Oxfordian or Kimmeridgian species (Aitkenhead 1975; Bibby 1966). There is some possibility, therefore, of a correlation with the disturbed zone at Ablation Valley (text-fig. 9; Table 2), but this must be regarded as tentative.

4. A small collection of poorly preserved marine invertebrates from Low Island, South Shetland Islands (text-fig. 1), contains an inoceramid that can probably be referred to *R. haasti* (M. R. A. Thomson, pers. comm.). The fossils occur in a thick sequence of volcaniclastic sediments which accumulated in a basin adjacent to an active island arc (Smellie 1980). The stratigraphy of these sediments is complex and at present their total thickness is unknown. However, they are at least partly Late Jurassic in age (Smellie 1980), and when the precise level of the fossiliferous horizon containing the specimen of (?) *R. haasti* has been determined, it will be possible to correlate the sequence directly with the Alexander Island succession.

5. Although no precise correlations can yet be made between the Fossil Bluff Formation of Alexander Island and the Jurassic Latady Formation, which crops out extensively in the region immediately to the south of the peninsula (text-fig. 1), a tentative comparison between these two major sedimentary units can be attempted. The Latady Formation, which is predominantly composed of fossiliferous, shallow-water volcaniclastic sediments, can be traced from the Lyon Nunataks-Behrendt Mountains region (eastern Ellsworth Land) northwards through the Orville and Lassiter coasts. The most detailed palaeontological studies of it to date have been carried out in the former of these regions; Quilty (1970) has recorded Middle Bajocian, Lower Callovian, and Oxfordian ammonites, and Stevens (1967) and Quilty (1977) Kimmeridgian belemnites and bivalves. *Retroceramus galoi* is common in this region and the overwhelming affinities would appear to be with the Heterian stage of New Zealand (Quilty 1977). So far, only preliminary palaeontological investigations have been carried out on the Orville and Lassiter coasts, but in both these regions there are

good indications of extensive Late Jurassic faunas (Rowley 1978; Thomson *et al.* 1978; Rowley and Williams, in press). On the Orville Coast there are perisphinctid-dominated ammonite assemblages with Kimmeridgian–Early Tithonian affinities (Thomson 1980) and large, coarsely-ribbed inoceramids that can almost certainly be referred to both *R. haasti* and *R. subhaasti.* A Kimmeridgian–Tithonian (or Ohauan) age for the Orville Coast faunas is strongly supported by the widespread occurrence of the bivalve *Malayomaorica malayomaorica* (Krumbeck). An easterly 'younging' trend through the Latady Formation from the Middle Jurassic and Early Kimmeridgian (Heterian) faunas of the Lyon Nunataks–Behrendt Mountains region to the later Kimmeridgian and Tithonian (Ohauan) faunas of the Orville Coast is further emphasized by the occurrence of berriasellid ammonites at Cape Zumberge, the most easterly extremity of the Orville Coast (Thomson 1980). These ammonites may well correlate with the berriasellid zone exposed in the lower levels of the Fossil Bluff Formation of Alexander Island (text-fig. 9). At present, it would appear that the Latady Formation faunas essentially predate those of the Fossil Bluff Formation; perhaps there is no more than approximately 500 m of stratigraphical overlap between the two units (Table 2 and text-fig. 9).

Regional correlations

Spiti. Recent work on the ammonite faunas from the lower levels of the Fossil Bluff Formation has shown that there are very strong links with the Late Jurassic ammonites of the Spiti Shales of the Himalayas (Thomson 1979). The Middle Spiti Shales are characterized by a distinctive perisphinctid assemblage in which the genera *Virgatosphinctes* and *Aulacosphinctoides* predominate, and this compares well with the assemblage present in the Ablation Valley section between 125 and 400 m (text-fig. 9) (Arkell 1956; Thomson 1979). The Upper Spiti Shales contain genera such as *Spiticeras*, *Berriasella*, *Blandfordiceras*, *Himalayites*, *Kossmatia*, *Kilianella*, *Sarasinella*, and *Bochianites* (Arkell 1956, p. 407), and can be correlated with the Ablation Valley section above the 400 m level, with the whole of the Callisto Cliffs section, and with the Tombaugh Cliffs section below the 271 m level (text-fig. 9). This correlation is strengthened by the occurrence of *R. everesti* in the Upper Spiti Shales, Callisto Cliffs, and Tombaugh Cliffs.

The Lower Spiti Shales, containing *Belemnopsis uhligi* Stevens, *B. alfurica* (Boehm), and several ammonites with Oxfordian affinities, have a probable age range of Upper Oxfordian–Middle Kimmeridgian (Stevens 1965, p. 149). A large, coarsely ribbed inoceramid from the same beds has been identified as *Inoceramus* cf. *sularum* (Holdhaus 1913, p. 420), but it has already been suggested (p. 566) that this specimen may in fact belong within *R. haasti.* The occurrence of *B. alfurica*, ammonites with Oxfordian affinities, and an inoceramid which is perhaps close to *R. haasti*, all suggest a possible correlation of the Lower Spiti Shales with the disturbed zone in the Ablation Valley section (text-fig. 9).

Thus, the Lower, Middle, and Upper Spiti Shales can be directly correlated with the lower levels of the Fossil Bluff Formation in eastern Alexander Island (text-fig. 10). However, there is very little precise stratigraphical information available for the Spiti sequence and no detailed comparisons can be made between the two areas. The majority of the Spiti specimens are unlocalized, and there are, as yet, no accurately measured sedimentary successions available for correlation purposes (Arkell 1956; Helmstaedt 1969; Mouterde 1971).

New Zealand. The Late Jurassic deposits of New Zealand have been divided into three stages: the Heterian, Ohauan, and Puaroan (see, e.g., Marwick 1953; Stevens and Speden 1978). *Retroceramus galoi* serves as a useful indicator for the Heterian, in which there are also three ammonite zones (the *Epicephalites*, *Idoceras*, and *Kossmatia* zones, in ascending order); the boundary between the latter two zones has been taken to coincide with the Lower–Middle Kimmeridgian boundary (Arkell, *in* Fleming and Kear 1960). The *Kossmatia* zone continues into the overlying Ohauan stage, which is characterized by *R. haasti.* The distinctive specimen of *Inoceramus* sp. cf. *subhaasti* (= *R.* sp. nov. 2) occurs just above the Heterian–Ohauan boundary in the Lower Kowhai Point Siltstone (Fleming and Kear 1960).

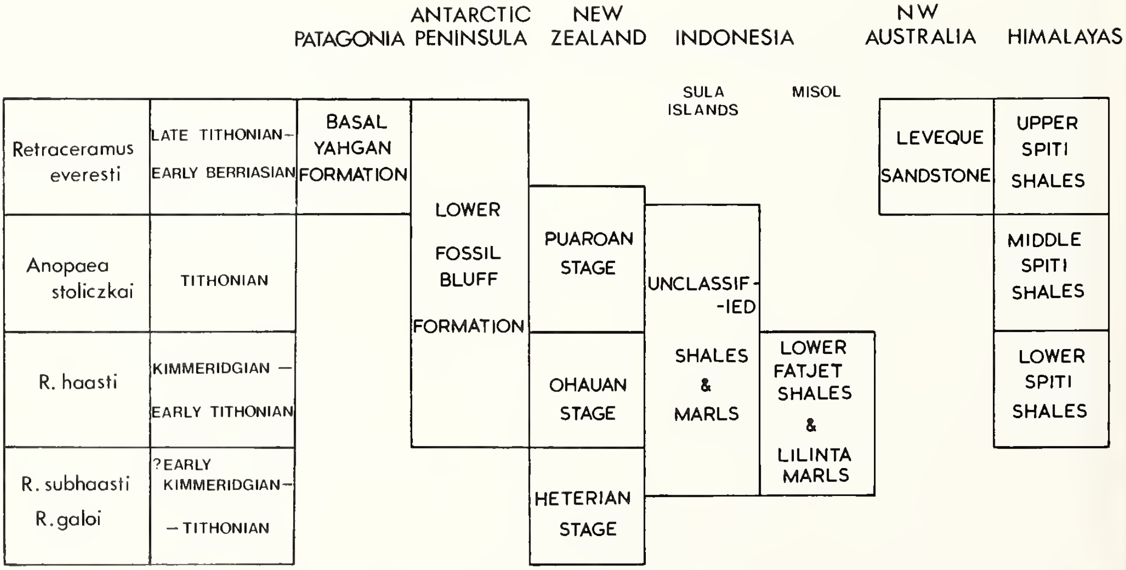
Two ammonite zones can be recognized in the Ohauan stage; a *Kossmatia* zone (continued from the top of the Heterian) and a later *Paraboliceras* zone (Arkell, *in* Fleming and Kear 1960). The latter passes up into an *Aulacosphinctoides* zone which marks the transition from Middle

Kimmeridgian to Lower Tithonian strata, and the beginning of the Puaroan stage (e.g. Stevens 1965, fig. 13; Speden 1970, table 1). This *Aulacosphinctoides* zone may be particularly useful for overseas correlations as it appears to have species in common with both Antarctica and Spiti. One specimen of *A.* aff. *sparsicosta* (Uhlig) from the 125–400 m zone at Ablation Valley (text-fig. 9) is close to the Puaroan species *A. brownei* (Marshall) (Thomson 1979, p. 22), and there may be several species of *Aulacosphinctoides* and *Uhligites* in common between the Puaroan stage and the Middle Spiti Shales (Stevens and Speden 1978, p. 268).

The Puaroan stage in New Zealand consists of a basal sequence of interbedded sandstones and conglomerates which passes up into a thick sequence of fossiliferous siltstones (the Puti Siltstones). The total thickness of the stage is approximately 1500 m (Stevens and Speden 1978, fig. 18). *Aulacosphinctoides brownei* ranges through most of the stage, but *R.* aff. *everesti* is restricted to the topmost levels (Stevens 1965, fig. 13). Other characteristic fossils include several species of *Buchia* and belemnites of the *B. uhligi* complex (Stevens and Speden 1978; Stevens 1965).

As no precise match can be made between the faunas of the Fossil Bluff Formation and those of the Heterian stage, it is likely that the latter (containing *R. galoi*) correlates with a level below that of the lowest exposed level in eastern Alexander Island (text-figs. 9 and 10). The overlying Ohauan stage contains *R. haasti* and thus correlates with at least part of the disturbed zone in the Ablation Valley section (text-figs. 9 and 10). In New Zealand, *R. haasti* occurs in the Lower Ohauan, between the *Kossmatia* and *Paraboliceras* zones (Stevens 1965, fig. 13).

The presence of a distinctive *Aulacosphinctoides* assemblage suggests that the Puaroan stage can be correlated with a fairly low level in the Fossil Bluff Formation (text-figs. 9 and 10). However, this *Aulacosphinctoides* zone is almost certainly much more extensive than the one exposed in Ablation Valley as it extends through several hundreds of metres of strata (Stevens 1965, fig. 13). *Retroceramus* aff. *everesti* occurs near the top of the Puaroan stage, which has traditionally been regarded as no younger than Middle Tithonian (e.g. Stevens 1965; Speden 1970). Thus, the Puaroan stage as a whole, which also contains belemnites of the *B. uhligi* complex and species of *Hibolithes* (Stevens 1965), correlates with approximately the middle levels of the Ablation Valley section and lower levels of the Callisto Cliffs section (text-figs. 9 and 10). The presence of *Aulacosphinctoides*,



TEXT-FIG. 10. Regional correlations in the Late Jurassic of the Southern Hemisphere. The stratigraphic units in each region have been correlated using the inoceramids listed at the left-hand side of the figure and associated ammonites and belemnites. Full details of the correlations are given in the text.

R. aff. *everesti* and belemnites of the *B. uhligi* complex suggests that it can also be correlated with the Middle Spiti Shales (Stevens 1965). In New Zealand, strata of Puaroan age are overlain by an essentially non-marine sequence (the Huriwani Formation) which probably spans the Jurassic-Cretaceous boundary (Stevens and Speden 1978).

It must be emphasized that the outline of New Zealand stratigraphy presented so far is essentially the conventional one based on the ammonite identifications of Arkell (*in* Fleming and Kear 1960) and the belemnite and buchiid bivalve determinations by Stevens (1965) and Fleming (1959), respectively. It has already been mentioned (p. 567) that an alternative view of the New Zealand Late Jurassic stratigraphy places the greater part of the entire sequence within the Late Tithonian. Enay (e.g. 1973) believes that there is no Early Tithonian in any part of the Indo-Pacific province, and that assemblages containing ammonites such as *Kossmatia*, *Paraboliceras*, and *Aulacosphinctoides* should all be regarded as Late Tithonian. Applying Enay's (1973) views to the New Zealand succession implies that the Heterian *Kossmatia* zone, and all succeeding zones, are Late Tithonian in age. As the Lower Heterian *Idoceras* and *Epicephalites* zones are presumably still assigned to the Lower Kimmeridgian, there must be a considerable non-sequence (spanning perhaps the whole of the interval between the Middle Kimmeridgian and the Middle Tithonian) within the Heterian stage. However, there is little evidence of a major break within the stratigraphical succession, and the existence of such a large diastem in the New Zealand Late Jurassic is questionable (Stevens and Speden 1978, p. 267). Obviously, the precise relationships of the New Zealand Late Jurassic stages to the international stratigraphical divisions have yet to be fully resolved (Stevens and Speden 1978, p. 267).

Indonesia. There is considerable potential for including the Late Jurassic inoceramid faunas of Indonesia within the zonation scheme outlined above. Preliminary investigations in the Sula Islands suggest that *R. galoi*, *R. subhaasti*, and *R. haasti* all occur within a 100–150 m sequence of silty shales that has an approximate age range of Kimmeridgian-Middle Tithonian (Westermann *et al.* 1978, p. 98). These beds, which also contain species of *Belemnopsis*, *Buchia*, and *Malayomaorica*, as well as occasional perisphinctid ammonites, can be tentatively correlated with the Lower Spiti Shales, the Ohauan stage of New Zealand, and the disturbed zone in the Ablation Valley section of Alexander Island (text-fig. 10). Overlying the silty shales is a sequence of marly claystones (100–500 m thick) containing *Haplophylloceras*, *Blandfordiceras*, *Virgatosphinctes*?, indeterminate haploceratids, phylloceratids, and lytoceratids, and the bivalves *Buchia* cf. *plicata* Zittel and *Anopaea*? *stoliczkai* (Westermann *et al.* 1978). The occurrence of the last-named species, together with an ammonite assemblage that includes both *Virgatosphinctes*? and *Blandfordiceras*, suggests a possible correlation with the level of the *Virgatosphinctes-Aulacosphinctoides* zone in the Ablation Valley section (text-fig. 9). This zone can be further correlated with the Middle Spiti Shales and the Lower Puaroan stage of New Zealand (text-fig. 10).

The occurrence in Misol of *R. subhaasti* in the Lilinta Marls and *R. haasti* in the Lower Fatjet Shales (Stevens 1965, table 13) suggests that these two rock units can be correlated with the Kimmeridgian-Middle Tithonian shales of the Sula Islands (text-fig. 10). However, the overlying Upper Fatjet Shales and Lower and Upper Fatjet Limestones apparently lack diagnostic fossils and cannot be readily correlated with beds in other regions.

New Guinea, New Caledonia, Timor, and Western Australia. Correlation by inoceramid biozones can also be extended to include the Late Jurassic deposits of regions such as New Guinea, New Caledonia, Timor, and Western Australia. Members of the *galoi-subhaasti-haasti* group of species probably occur in both New Guinea and New Caledonia (Glaessner 1945; Avias 1953; Routhier 1953; Stevens 1965; Skwarko 1967; see pp. 564, 566), and *R. haasti* is present in Timor (pp. 564, 566; Krumbeck 1923).

The presence of *Inoceramus* sp. nov. *a*, *b*, and *c* (= *R. everesti*) in the Leveque Sandstone of Dampier Land, Western Australia (Brunnschweiler 1960), may be particularly useful for correlating the Late Jurassic-Early Cretaceous deposits of the Canning Basin with those of other areas. The first prominent Late Jurassic deposit in the Canning Basin, the Alexander Formation, consists of at least 70 m of siltstone with fine interbedded shale layers (Veevers and Wells 1961). It contains ammonites which have been tentatively identified as belonging to the genera *Virgatosphinctes* and *Kossmatia* (Ludbrook 1978, p. 224) and can probably be dated as Kimmeridgian–Early Tithonian (Veevers and Wells 1961). The oldest beds exposed in the Dampier Peninsula, the Langey Beds, have yielded specimens of *Belemnopsis* cf. *aucklandica* (Hochstetter), *B.* cf. *alfurica* (Boehm), *Kossmatia* cf. *tenuistriata* (Gray), and *Malayomaorica malayomaorica* (Krumbeck): they thus have a probable age range of Middle Kimmeridgian–Middle Tithonian (Brunnschweiler 1960), and may perhaps be taken to post-date the Alexander Formation (Ludbrook 1978, table 1). The Langey Beds pass up into the extensive Jowlaenga Formation (at least 230 m of sandstones and siltstones) which contains both Late Jurassic and Early Cretaceous faunal elements (Brunnschweiler 1960, p. 37). The succeeding Broome Sandstone is at least 300 m thick, but may be, in part, laterally equivalent to the Jowlaenga Formation (Veevers and Wells 1961). It is essentially a non-marine deposit and contains fossil plants with both Late Jurassic and Early Cretaceous affinities. The Leveque Sandstone, from which the specimens of *R. everesti* were collected (Brunnschweiler 1960), is believed to overlie the Broome Sandstone, but is known from only one isolated locality (where it is 10 m thick) (Brunnschweiler 1960; Veevers and Wells 1961). It has been assumed to be Neocomian, largely on the alleged affinities of its inoceramid fauna (Brunnschweiler 1960), but *R. everesti* is now known to transgress the Jurassic–Cretaceous boundary (p. 583), and it would appear that the Leveque Sandstone could equally well be Late Jurassic or Early Cretaceous (or both) in age (text-fig. 10).

South America. Although the former geological continuity of southern South America, the Scotia Arc, and the Antarctic Peninsula has now been established beyond doubt (see, e.g., Barker and Griffiths 1972, 1977), very few palaeontological correlations have been attempted between these now widely separated regions. This is partly due to the lack of detailed stratigraphical studies in certain key areas (especially in South America), and partly to the different tectonic settings of the major sedimentary basins. Whereas the Fossil Bluff Formation, in which comparatively shallow shelf sediments predominate, accumulated in a fore-arc or intra-arc basin, both the Cumberland Bay Formation of South Georgia and Yahgan Formation of southern Patagonia accumulated in an extensive back-arc basin (e.g. Suárez and Pettigrew 1976, fig. 7; Dott, Winn and Smith, in press, fig. 1). Deep-water turbidite facies predominate in both the latter formations and fossils are rare. However, Katz and Watters (1966) recorded several specimens of *Inoceramus* sp. (= *R. everesti*) from the Yahgan Formation of Navarino Island, and these may be of considerable importance for regional correlations (text-fig. 10).

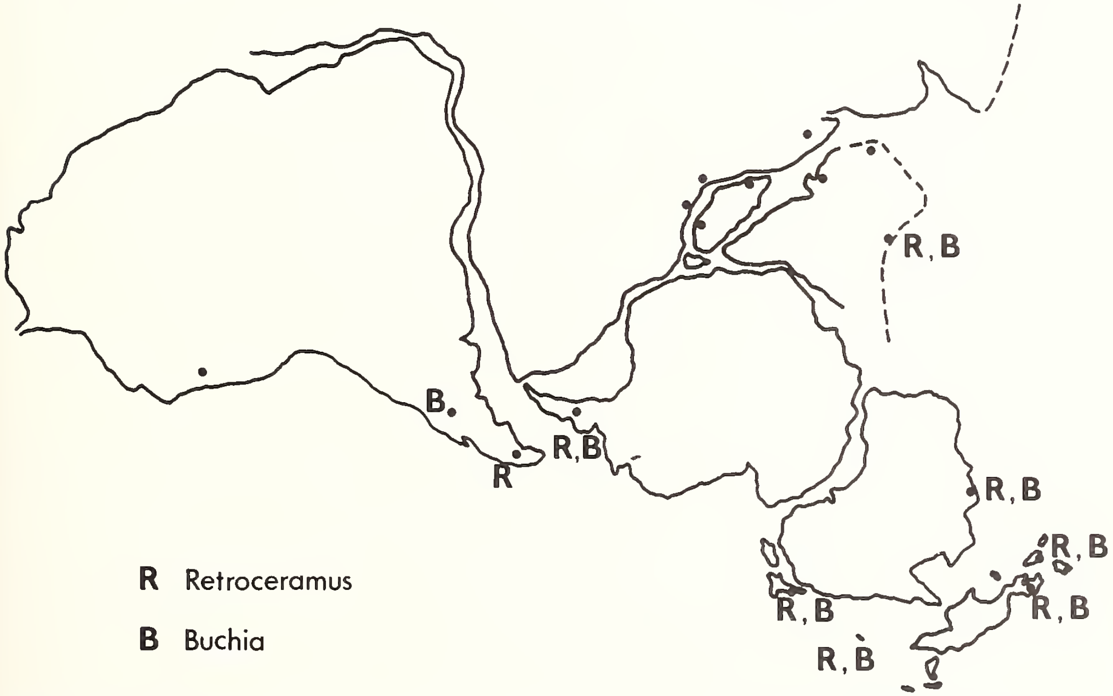
The Yahgan Formation is predominantly composed of volcaniclastic turbidites and shales, and has a total thickness in the region of 4–5 km. Its base is probably within the Late Jurassic, but it ranges up into well within the Neocomian (Winn 1978, p. 537). Although well exposed on Navarino Island, the Yahgan Formation cannot be accurately defined, and no type section has yet been established for it (Katz and Watters 1966). Judging from their occurrence between two prominent sills (Katz and Watters 1966, figs. 15 and 16), the specimens of *Inoceramus* sp. probably occur at least 1000 m above the base of an estimated 3000 m sequence, but no other distinctive faunal horizons have been recognized.

Strata of equivalent age to those of the Yahgan Formation can be traced further north in Patagonia along the Chile–Argentina border. Fossiliferous mudstones occur in both the Ultima Esperanza and Lago Argentina regions (Feruglio 1936, 1949; Dott *et al.*, in press), but again, very few specimens can be precisely localized. This is unfortunate, for the latter region has yielded a fossil assemblage that shows strong similarities to that found in parts of the Ablation Valley section of eastern Alexander Island. This assemblage, collected from the Cerro de los Fosiles (to the north of Estancia del Quemado), contains the ammonites *Aulacosphinctoides*, *Virgatosphinctes*, *Corongoceras*, *Berriasella*, *Blandfordiceras*, *Steueroceras*, and *Favrella*, as well as *Inoceramus* cf. *steinmanni* (= *R. everesti*) and *Belemnopsis patagoniensis* (Favre) (? = *B. gladiatoris* Willey 1973, p. 33) (Feruglio 1936, 1949, p. 169). It would appear that all the above-listed ammonites were collected

60-80 m above the base of a 1000 m section (Feruglio 1949, pp. 168-169). Approximately 200 m higher up in this section there is a *Holcoptychites* zone containing *Holcoptychites*, *Berriasella*, and *Acanthodiscus*, and 200 m above this a *Favrella* zone containing *Favrella*, *Phylloceras*, *Inoceramus anomaeformis* Feruglio, and *I.* aff. *posidonomyaeiformis* Maury (Feruglio 1936, 1949). The *Aulacosphinctoides-Virgatosphinctes-Berriasella* zone can be dated as Tithonian-Berriasian, and the *Holcoptychites* and *Favrella* zones as Berriasian, but it must be emphasized that the stratigraphy in this region can at best only be regarded as tentative. In a reappraisal of Feruglio's (1936) material, Leanza (1967) indicated that at the Cerro de los Fosiles locality, *I.* cf. *steinmanni* (= *R. everesti*) occurs at a level above that of the *Aulacosphinctoides-Virgatosphinctes-Berriasella* zone, but no indication is given as to the extent of this separation. It can only be concluded that the Cerro de los Fosiles locality correlates in general terms with the lower levels of the Fossil Bluff Formation in eastern Alexander Island. More precise stratigraphical data are required before a detailed correlation is attempted.

DISTRIBUTION

At first sight, the occurrence of the genus *Retroceramus* in Antarctica might be taken as evidence for the existence of a Late Jurassic Southern Hemisphere Austral (or anti-Boreal) faunal realm. It was obviously an important component of many benthic assemblages, and when taxonomic studies of the Lassiter and Orville Coast faunas have been completed there may well be an equivalent diversity of species in Antarctica to that known from the Siberia-Alaska region. However, it will be apparent from the foregoing stratigraphical discussion that *Retroceramus* is, in fact, distributed around much of what were the margins of the ancient Gondwana supercontinent (text-fig. 11). It can be traced from South America through Antarctica to New Zealand, Indonesia,



TEXT-FIG. 11. The occurrence of the genera *Retroceramus* and *Buchia* in the Southern Hemisphere. Black dots indicate localities where Late Jurassic bivalves have been collected: note the absence of both *Retroceramus* and *Buchia* from the Ethiopian province. The Late Jurassic reconstruction of Gondwana is based on that given by Smith and Briden (1977, Map 35).

North-west Australia, and the Himalayas, as indeed can other 'Boreal' genera such as *Buchia* and *Anopaea* (Fleming 1959; Stevens 1965; Quilty 1977; Taylor *et al.* 1979; Crame 1981*b*). These occurrences over a considerable latitudinal range (text-fig. 11) argue against any purely climatic control of distribution and suggest instead that there may well have been some form of control by the prevalent environments of deposition. The southern margins of Gondwana in the Late Jurassic were essentially formed by a series of narrow and deep tectonic basins comprising the so-called circum Gondwana geosynclines (see, e.g., Fleming 1979, fig. 2, and Audley-Charles 1978, fig. 3). Shelves along the inner edges of these basins would have sloped comparatively steeply into deep water and many appear to have been subjected to both high rates of sedimentation and periods of tectonic instability (see, e.g., Taylor *et al.* 1979, p. 38; Bell 1975). It would seem that the benthic faunas best able to cope with these sorts of conditions were low diversity-high abundance assemblages in which epifaunal bivalves (especially inoceramids and buchiids) predominated. Inoceramids and buchiids are conspicuously absent from the coeval Southern Hemisphere Ethiopian province (text-fig. 11), which was centred on a shallow epicontinental sea.

CONCLUSIONS

1. Most of the inoceramid bivalves occurring in Southern Hemisphere Late Jurassic temperate realm assemblages can be assigned to the genus *Retroceramus*. Typically obliquely elongated, equivalve, and bearing patterns of simple concentric ornament, *Retroceramus* can often be distinguished from *Inoceramus* on the basis of external morphology alone. However, a further diagnostic feature is available in the structure of the respective ligament areas. In *Retroceramus* the ligament pits are typically large, rounded-rectangular to oval in outline, and somewhat irregular in their distibution, whereas in *Inoceramus* they are narrow and elongated, and are typically arranged in a uniform series set adjacent to the hingeline.

A few Late Jurassic species cannot be easily assigned to either *Retroceramus* or *Inoceramus*, and some, such as *R. everesti* (Oppel), may be intermediate forms between the two genera. Similar problems in establishing clear-cut generic boundaries are encountered in other epifaunal bivalve groups (such as the Mytilidae—see Newell 1942).

2. *Retroceramus* was replaced by *Inoceramus* in the Early Cretaceous and it is thought that this change may be linked to the widespread assumption at this time of the epibyssate habit by inoceramids. Functional interpretations suggest that *Retroceramus* was an essentially endobyssate genus but that Early Cretaceous *Inoceramus* species were predominantly epibyssate. This fundamental change in life habit enabled new substrate types to be occupied and a variety of growth forms to be adopted, and thus paved the way for the progressive diversification of *Inoceramus* through the Cretaceous. This represents one of a series of major endo- to epibyssate life habit transitions which occurred during the evolutionary history of the Inoceramidae. Such transitons are probably best explained as a sequence of neotenous oscillations.

3. Four common species of *Retroceramus* (*R. galoi*, *R. subhaasti*, *R. haasti*, and *R. everesti*) can be recognized in Kimmeridgian to Tithonian strata in the Southern Hemisphere. Each of these species is characterized by a considerable degree of morphological variation and it is possible that future studies may permit the establishment of a number of subspecies. These four species occur in consistent stratigraphical succession around the southern margins of Gondwana and form the basis of an inoceramid biozonation scheme that can be used for both local and regional correlations. Small, isolated exposures within the Antarctic Peninsula can be correlated with the Fossil Bluff Formation of Alexander Island and in time it should be possible to correlate the latter unit in detail with the extensive Latady Formation of the Lassiter and Orville coasts, and eastern Ellsworth Land. Use of the same inoceramid biozones, together with those based on associated cephalopods, suggests that the lower levels of the Fossil Bluff Formation correlate with the Lower, Middle, and Upper Spiti Shales of the Himalayas and with the Ohauan and Puaroan stages of New Zealand. Correlations can also be extended to South America, New Caledonia, New Guinea, Indonesia, Timor, and Western Australia.

Late Jurassic inoceramid bivalves from western Antarctica offer considerable scope for further palaeobiological and biostratigraphical investigations. However, care must be exercised in the identification of species, for there are a number of apparent instances of homeomorphy between Middle and Late Jurassic forms. When taxonomic studies have been completed, western Antarctica should become one of the standard stratotypes for Late Jurassic inoceramid bivalves.

4. Although the Boreal bivalve genera *Retroceramus*, *Buchia*, and *Anopaea* are common in the Late Jurassic of western Antarctica, their presence does not necessarily indicate the existence of a Southern Hemisphere anti-Boreal faunal realm. Closer examination of the distribution of these three genera reveals that they can, in fact, be traced around much of what were the southern margins of Gondwana. Their distribution seems to have been controlled primarily by the prevalent sedimentary facies, rather than by the existence of any pronounced climatic zonation.

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THE DEVONIAN PLANT *REIMANNIA*, WITH A DISCUSSION OF THE CLASS PROGYMNOSPERMOPSIDA

by WILLIAM E. STEIN, JR

ABSTRACT. The type specimen of *Reimannia aldenense*, from the Middle Devonian of New York, was reinvestigated in order to more critically evaluate the anatomy of this poorly understood monotypic genus. Three successive axis orders were observed in organic connection. The first-order axis contains a three-ribbed primary xylem column showing mesarch order of maturation with protoxylem strands along median-radial planes and near the tips of primary xylem ribs. Traces appear to be produced in a helical arrangement. The primary xylem of the second-order axis is proximally elliptical or shallowly four-ribbed, as seen in transverse section, and gives off a sub-opposite pair of traces, supplying third-order axes, which may divide once through the course of their departure. Distally, the primary xylem of the second-order axis assumes an increasingly three-ribbed configuration and probably gives off a single abaxial trace. No evidence for a histologically distinctive 'peripheral loop' has been found.

Although placed within the Iridopteridineae by Arnold (1940), these features show that *Reimannia* has little in common with the other genera of this group. Instead, *Reimannia* should be considered a form genus for permineralized axes within the Aneurophytales (Progymnospermopsida). Assignment is made to this group even though *Reimannia* shows neither of the diagnostic characters originally used in combination to establish the class: a free-sporing habit and 'typically gymnospermous' secondary vascular tissues. It is pointed out that the definition of the Progymnospermopsida, based upon a combination of primitive and derived characters, is inextricably tied to a prior phylogenetic assessment as the direct ancestors of seed plants. Although such a definition is acceptable on methodological grounds, primitive and derived characters should not be treated equally in the analysis of phylogeny or in the characterization of groups.

REIMANNIA ALDENENSE was established by Arnold (1935) for well-preserved material from the Middle Devonian Ledyard Shale Member of the Ludlowville Formation near Alden, Erie County, New York. Although Arnold referred to several specimens found in more than one concretion (1935, p. 5), the type material consists of axes in a single concretion and apparently this alone formed the basis of his description. Axes of more than one size were included in *Reimannia* but primary emphasis was placed on a single small axis showing the best preservation (Arnold 1935, figs. 1, 6, 9, text-fig. 1). Arnold considered the essential features of *Reimannia* to include: (1) a three-angled primary xylem strand, (2) three protoxylem strands, one of them an 'apparent peripheral loop' (Arnold 1935, p. 7), and (3) the absence of secondary tissues. The three-ribbed configuration of the primary xylem reminded Arnold of *Aneurophyton germanicum* (Kräusel and Weyland 1923, 1926, 1929) but the peripheral loop suggested to him also affinities with the Zygopteridaceae, and doubt was expressed whether real affinities could be determined for such fragmentary material. Subsequently, with the establishment of *Arachnoxylon* (Read 1938) and the discovery of *Iridopteris* (Arnold 1940), Arnold (1940, 1947) placed *Reimannia* in a new suborder, the Iridopteridineae, within the Coenopteridales as a second genus in the family Iridopteridaceae. The presumed occurrence of a peripheral loop, although not well documented in any of these plants, was considered of prime importance in assessing their affinities. *Reimannia* was proposed as an intermediate between *Arachnoxylon* and *Iridopteris* in a morphological series linking primitive Devonian psilophytes with the coenopterid ferns of the Upper Devonian and Carboniferous (Arnold 1947).

In 1939 Read and Campbell named a second species of *Reimannia*, *R. indianensis*, for a small axis collected from the lower Mississippian (Tournasian) Falling Run Member of the Sanderson

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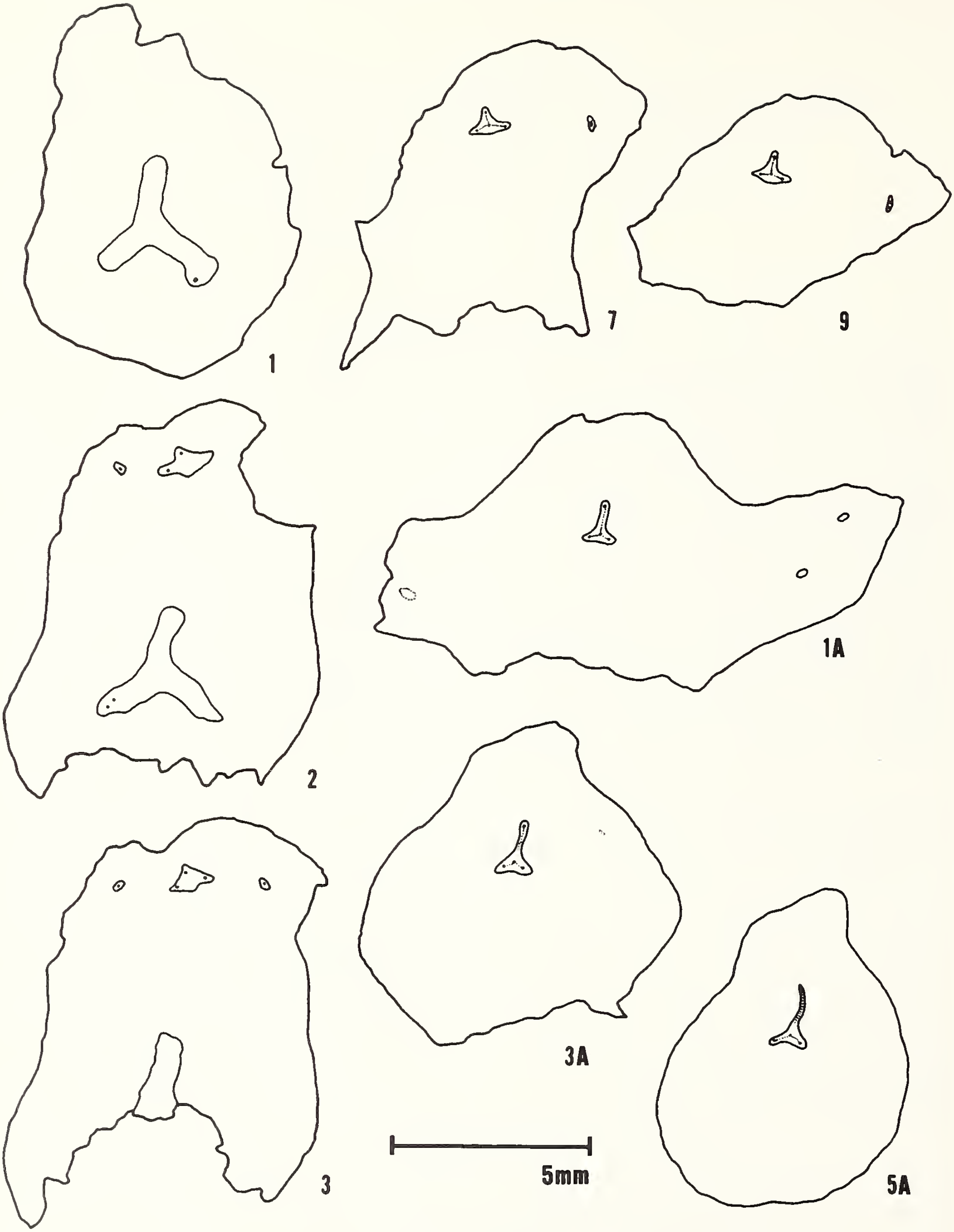


TEXT-FIG. 1. Type specimen of *Reimannia aldenense* Arnold. *Camera lucida* drawings showing organic connection of the three axis orders, the positions of traces in the specimen, and the changes in the configuration of the primary xylem at different levels of the second-order axis. Section numbers are located beside each drawing. Sections 1–3 include portions of the first-order axis and sections 7–5A include only the second-order axis and associated traces to the third order.

Formation of the New Albany Shale in Indiana. This assignment was based upon only a superficial similarity with the smaller axis of *Reimannia*, as described by Arnold, particularly the presence of a three-ribbed or T-shaped primary xylem column with mesarch order of maturation. Hoskins and Cross (1951) rightly segregated *R. indianensis* into its own genus, *Reimanniopsis*, citing differences in the configuration of the stele and in the amount of cortex, as well as the absence of traces in *Reimanniopsis*. Subsequently, Beck (1960*a*) suggested a possible relationship between *Reimanniopsis* and *Stenokoleos*.

Using evidence from the type specimen and photographs supplied by Arnold, Hoskins and Cross (1951) also redescribed certain aspects of the smaller axis of *R. aldenense*. They pointed out the presence of a fourth protoxylem strand near the centre of the xylem column, and suggested a helical order of trace departure. In addition, these authors expressed the belief that the peripheral loop in this specimen represented an incipient trace near the level of its departure from the primary xylem of the axis. Leclercq (1970), in de-emphasizing the importance of the peripheral loop as a taxonomic character in the face of a suite of other diagnostic features circumscribing the Cladoxylopsida, carried the idea even further. Pointing to *Reimannia* as a plant containing both a peripheral loop and normal protoxylem strands, she suggested that the peripheral loop may have had its evolutionary origin as a discontinuous column or strand of protoxylem parenchyma intimately associated with trace departure.

In 1974 Scheckler noted that since Arnold's original description of *R. aldenense*, several apparently unrelated plants had been discovered in Middle and Upper Devonian sediments containing three-ribbed protosteles including aneurophytalean progymnosperms, and a Devonian *Stenokoleos*.

Without consulting the type material, Mustafa (1975) included *R. aldenense* in a sweeping synonymy of Devonian taxa including *Rellimia* (*Protopteridium*) (Leclercq and Bonamo 1973), *Aneurophyton*, *Reimanniopsis*, and *Triloboxylon* (*Aneurophyton hallii*) *arnoldii* (Arnold 1940; Matten 1974). The resultant taxon, called *Protopteridium thomsonii*, was assigned to the Aneurophytales of the Progymnospermopsida. However, the characters used in support of this synonymy (helical arrangement of branches and three-ribbed steles) have been viewed by other workers (Bonamo 1977; Serlin and Banks 1978) as insufficiently diagnostic in light of known differences between the taxa in other aspects of their morphology.

I became interested in *Reimannia* while comparing the type specimen with other members of Arnold's Iridopterideae and with possible new representatives of this group. In a view through the plastic in which the specimen had been embedded, I noticed that one axis bore a preserved lateral branch. Thus, a reinvestigation of this specimen promised to provide additional information on the three-dimensional architecture of this plant plus some direct evidence, perhaps, on the relationship between peripheral loop and incipient traces.

LOCALITY

According to Arnold (1935), *Reimannia aldenense* was collected from the well-known locality at Spring Creek, half mile north-east of Alden, Erie County, New York (Fisher 1951; Buehler and Tesmer 1963; Brett 1974). Plants occur in pyrite nodules of various sizes, along with a distinctive invertebrate fauna, in a narrow stratigraphic horizon of the Ledyard Shale Member, Ludlowville Formation, Hamilton Group. The horizon is upper Middle Devonian (Givetian). Besides *Reimannia*, plants recorded from this locality and horizon include *Triloboxylon* (*Aneurophyton hallii*) *arnoldii* (Arnold 1940; Matten 1974), *Xenocladia medullosina* (Arnold 1952), isolated fragments, occasionally very large, of secondary xylem referred to *Dadoxylon* Dawson (Arnold 1935, 1940), and a doubtful report of *Lepidodendron* (Fisher 1951).

MATERIALS AND METHODS

The single specimen consists of plant axes permineralized with iron sulphide, forming the nucleus of what was probably a nearly spherical pyrite concretion. When obtained for this study, the concretion had already been cut into two parts and both were embedded in plastic, thus maintaining the specimen in excellent condition. A total of three surfaces, all views of axes in transverse section, were prepared by Arnold (1935) and these alone formed the basis of his report. To the best of my knowledge, based upon personal communication with Dr. Arnold in 1977, and a thorough search of the collections of the Museum of Paleontology, University of Michigan, there are no additional fragments of the specimen. For this study, the individual nodule pieces were trimmed of excess plastic and accretionary pyrite. A total of twenty-one transverse sections were cut at 1 mm intervals except for one 1·5 mm thick section (no. 4), and a 2 mm thick end block (no. 11). All original surfaces prepared by Arnold have been conserved.

From two 1 mm thick transverse sections (no. 7A, no. 10), a total of nineteen longitudinal sections were cut at 1 mm intervals. One section (no. 4) was broken lengthwise several times and observed with scanning electron microscopy for details of pitting in tracheid walls preserved as pyrite casts. For discussions on the interpretation of these structures, see Grierson (1976), Stein (1981), and Beck, Coy and Schmid (1981). All cut sections were individually re-embedded in 'Bioplastic' (Ward's Scientific Establishment, Rochester, New York, U.S.A.). Most surfaces were prepared by grinding with no. 600 silicon carbide grit followed by fine-polishing with 0·05 mm aluminium oxide powder. A few were subjected to a concentrated nitric acid etch for 15 seconds, followed by neutralization with concentrated ammonium hydroxide, and a two step re-acidification of the specimen using hydrochloric acid following a technique similar to that described by Jennings (1972). For more specific information on this method, see Stein, Wight and Beck (1982).

DESCRIPTION

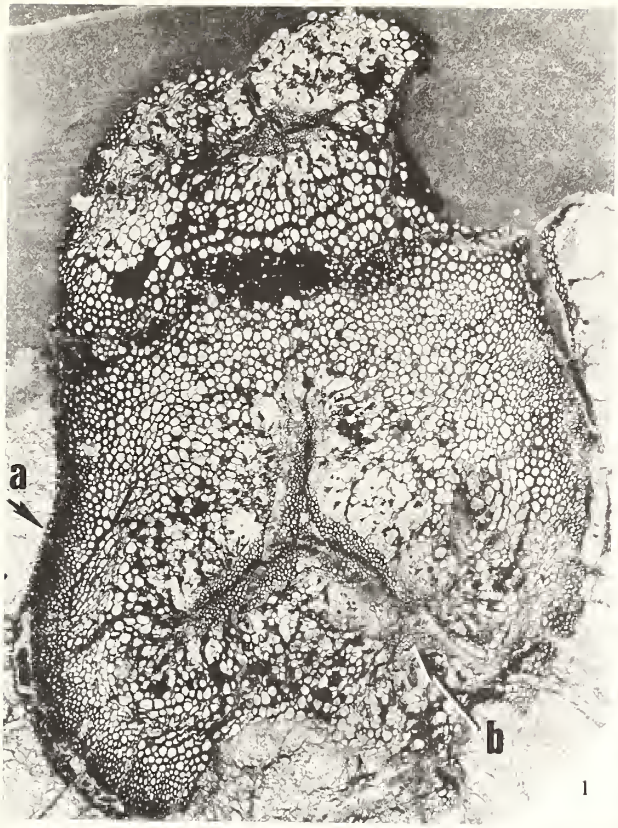
The type specimen provides evidence of three axis orders in organic connection (Pl. 60, fig. 1; Pl. 61, fig. 1; text-fig. 1). In transverse section, the first-order axis measures approximately 9·5 mm in diameter at its greatest extent and bears a second-order axis which is approximately 6·5 mm in diameter. The second-order axis, by far the most extensively preserved of the three orders, was observed over a distance exceeding 2 cm compared to a maximum length of 7 mm for the first-order axis fragment. Axes of the third order are preserved only at their bases and traces to this order have less than 1 mm preserved length. All orders are comprised of primary tissues only. Vascular tissues are protostelic with the primary xylem of first and second orders forming ribbed columns of tracheids. The primary xylem of traces to third-order axes is elliptical as seen in transverse section. External to the primary xylem at all levels is a poorly preserved region which probably represents primary phloem at least in part. Beyond this occurs an extensive and more or less homogeneous cortex. In some parts of the specimen, remnants of cells interpreted as epidermis are also present (see below).

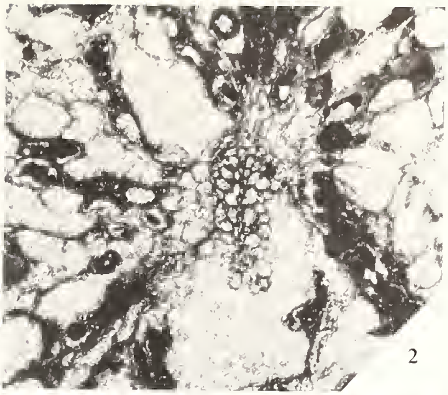
Cortex

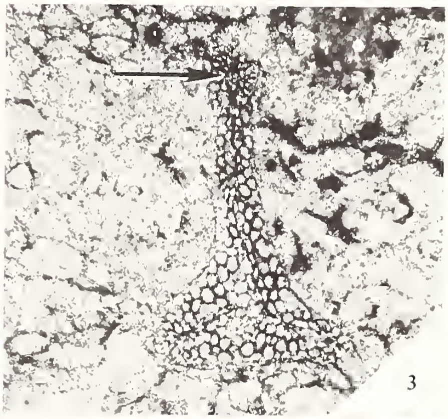
Cortex of the first-order axis (Pl. 1, fig. 1) measures from 1 to 3 mm in thickness with an average thickness of about 2 mm. The second-order axis (Pl. 61, fig. 1) has cortex only a little less extensive, ranging from 1·5 to 2·5 mm in thickness. There is no distinct zonation of cortical tissues although cells decrease in size and increase in apparent cell wall thickness toward the periphery of the axes (Pl. 61, fig. 3). Cellular specializations such as sclerotic nests, cortical secretory canals, or discrete fibrous hypodermal strands are not a feature of the specimen.

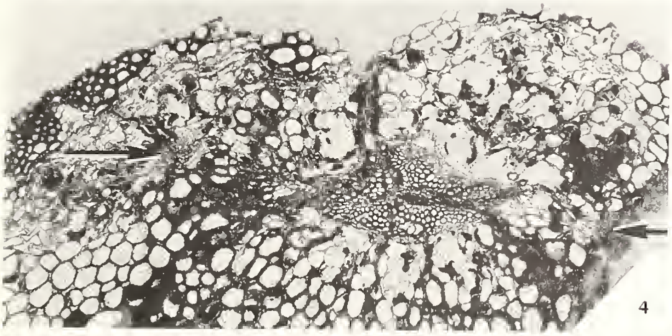
EXPLANATION OF PLATE 60

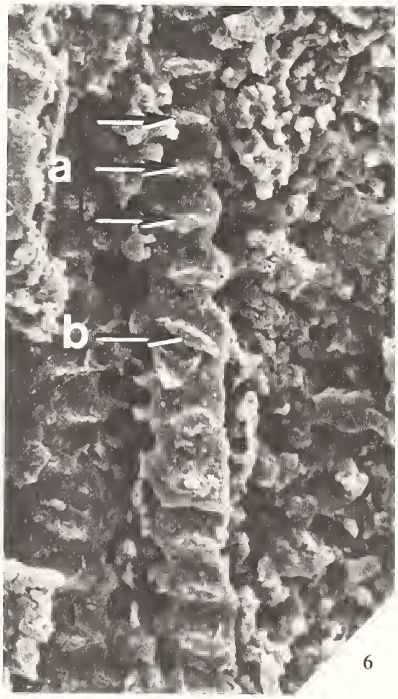
Figs. 1–6. *Reimannia aldenense* Arnold—type specimen from Erie County, New York. UMMP No. 16231. 1, transverse section of the first-order axis with attached proximal portion of the second-order axis. Note the three-ribbed configuration of the primary xylem in the first-order axis, and the four-angled shape of the primary xylem of the second-order axis. Compare with figs. 4, 5, and Pl. 61, fig. 1. Arrow **a** points to a bounding tissue interpreted as epidermis. Arrow **b** indicates the expanded tip of a primary xylem rib which represents an incipient trace at this level, × 10. 2, transverse section of a trace to the third axis order proximal to the level of its division into two traces, ×65. 3, transverse section showing three-ribbed configuration of second-order axis at about the level of Pl. 61, fig. 1. Arrow points to a protoxylem cavity probably associated with an incipient trace at this level, ×40. 4, transverse section, higher magnification of vascular tissues in second-order axis shown in fig. 1. Arrows indicate the sub-opposite pair of traces to third-order axes, ×20. 5, transverse section of second-order axis distal to the level in fig. 4. Note the increased prominence of the abaxial rib of the primary xylem and one of two traces to third-order axes, ×20. 6, split-longitudinal section observed by scanning electron microscopy showing the pyrite cast of a metaxylem tracheid with a column of discrete, elliptical aperture casts, arrows **a**. In one instance, an aperture cast leading into a cell lumen above the plane of the specimen surface can be recognized by the different orientation of its long axis, arrow **b**, ×1200.

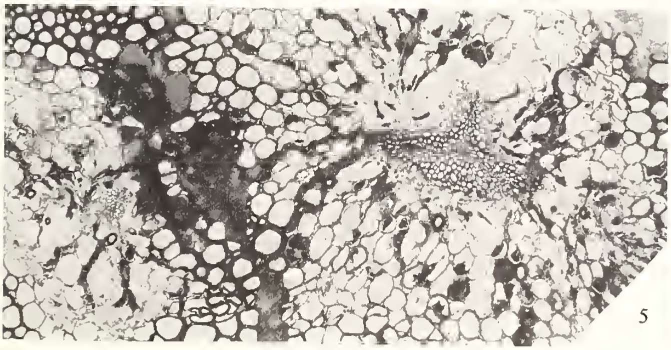












STEIN, *Reimannia*

Toward the centre of the axes, cortical cells range from 35 to 200 μm in diameter and are approximately isodiametric. At the periphery, they usually measure between 30 and 80 μm in transverse diameter but occasionally reach 100 μm. In longitudinal section, these cells appear sclerenchymatous and generally elongate. This outermost cortical layer has previously been interpreted as a fibrous hypodermis (Arnold 1935). Occasional cortical cells with dark materials in their lumina occur throughout most parts of the specimen, but are more common toward the centre of the axes (Pl. 60, figs. 1, 2, 5; Pl. 61, figs. 2, 3). They are generally lacking, however, in the outermost cortical regions (Pl. 61, fig. 3). On the basis of histological features other than the presence of the dark materials, these cells are not distinctive.

At the periphery of the preserved axes in some regions is a tissue apparently one, or at most two or three cell layers thick, which previously has been interpreted as an epidermis (Arnold 1935). Cell preservation is not sufficient, however, to enable one to recognize cuticle or to define the cells clearly on a histological basis. In transverse section, most of the cells appear isodiametric to slightly radially flattened. All are characterized by the presence of a large amount of a dark substance filling cell lumina (Pl. 60, fig. 1, arrow **a**; Pl. 61, fig. 3, arrow). These cells vary from 80 to 130 μm in transverse diameter, and are probably no more than twice the greater measurement in length.

Vascular tissues

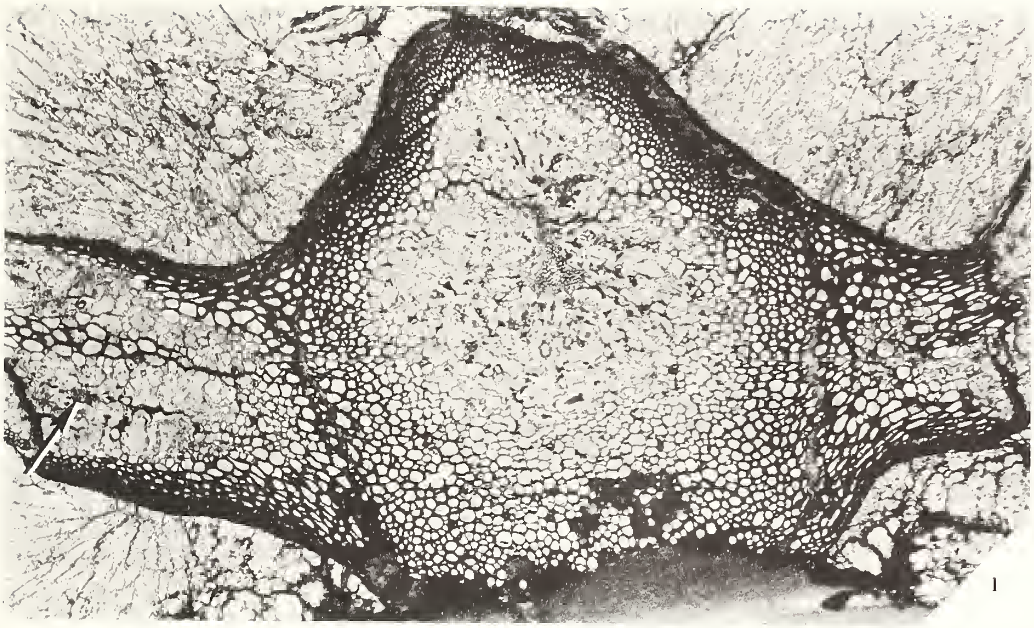
Elements of the primary xylem form a deeply three-ribbed column in the first-order axis (Pl. 60, fig. 1; Pl. 61, fig. 2). Primary xylem in the second-order axis is shallowly four-ribbed or diamond shaped proximally near the level of its departure from the first-order axis (Pl. 60, figs. 1, 4; Pl. 62, fig. 2), but becomes progressively more three-ribbed (Pl. 60, figs. 3, 5; Pl. 61, fig. 3; Pl. 62, figs. 1, 3). The maximum diameter of the primary xylem of the first order is approximately 3 mm with individual xylem ribs averaging 1·8 mm in radial extent, and 0·6 mm in width. In a distal portion of the second-order axis, the maximum primary xylem diameter varies from 0·8 to over 1·5 mm with primary xylem ribs varying in width from 0·1 to 0·3 mm, and in radial extent from 0·3 mm to as much as 1·3 mm in one case probably associated with the departure of a trace (Pl. 61, fig. 3; text-fig. 1).

Where well preserved, the primary xylem is apparently comprised only of conducting elements. At certain levels in the specimen, it is possible that isolated patches of xylem parenchyma were originally present (Pl. 61, fig. 2, arrow **a**). However, in most of these cases I have been unable to distinguish this possibility from the effects of poor preservation.

Primary xylem maturation was clearly mesarch. Although poorly preserved in the first-order axis, several probable examples of protoxylem strands were observed in the expanded tips of primary xylem ribs and also in a few positions internally along the median planes of some of the xylem ribs (Pl. 61, fig. 2). The peripheral protoxylem strands were probably associated with incipient traces but proof of this is lacking in the specimen. The positions of protoxylem strands in the primary xylem of the second-order axis have been determined with much greater precision. Proximally (Pl. 60, fig. 4; text-fig. 1, section 3), protoxylem strands occur near the tips of the lateral and abaxial ribs of the primary xylem. The adaxial rib of the primary xylem at this level is not associated with a protoxylem strand, and distally, it becomes indistinct. A fourth protoxylem strand is located at the centre of the primary xylem system in this axis. Although not obvious proximally, it is clearly present in distal sections (Pl. 60, fig. 5; Pl. 61, fig. 3; Pl. 62, figs. 1, 3). Between protoxylem strands along the median-radial planes, of xylem ribs, several very small and tangentially flattened or irregularly shaped tracheids can be seen in some transverse sections. These are interpreted as flattened elements of the metaxylem, and appear to be variable in expression but more prevalent in distal portions of the second-order axis (Pl. 61, fig. 3; Pl. 62, fig. 1). A single

EXPLANATION OF PLATE 61

Figs. 1–3. *Reimannia aldenense* Arnold—type specimen from Erie County, New York. UMMP No. 16231. 1, transverse section of the second-order axis distal to the level in Pl. 60, fig. 5, showing the bases of a sub-opposite pair of third-order axes. In the third-order axis base to the left, one of a pair of traces can be seen, arrow. Compare with text-fig. 1, × 10. 2, transverse section, higher magnification of primary xylem of first-order axis at a level near that of Pl. 60, fig. 1. Poorly preserved regions in the xylem, arrows **a**, suggest possible presence of xylem parenchyma. Arrow **b** indicates a partially preserved tissue immediately adjacent to the primary xylem interpreted as probable primary phloem, × 23. 3, transverse section of second-order axis distal to the level of fig. 1. The abaxial rib of the primary xylem is highly elongate at this level and probably associated with an incipient trace. Arrow points to the bounding tissue interpreted as epidermis in this specimen, × 20.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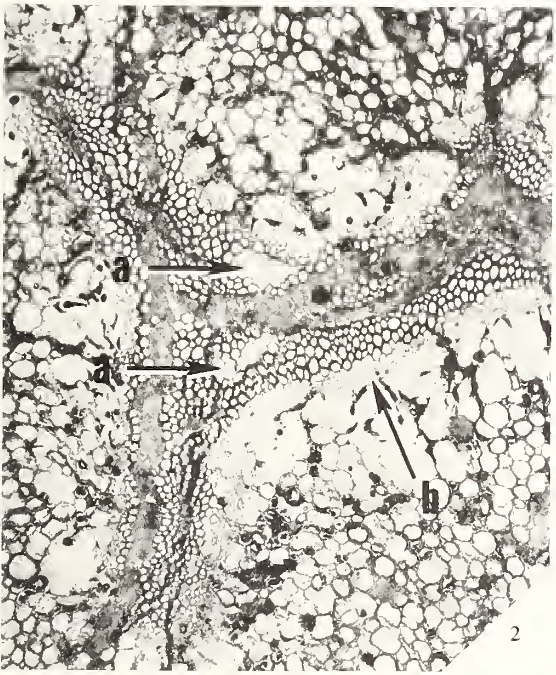

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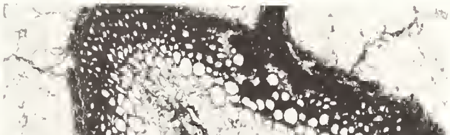
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STEIN, *Reimannia*

central protoxylem strand occurs in traces to the third-order axes (Pl. 60, figs, 2, 4). These divide once, tangentially with respect to the second-order axis, in association with division of the traces themselves.

All available evidence suggests that protoxylem strands are of a type which is typical of most vascular plants (for example, see Pl. 62, fig. 2, arrow, 3). In some cases (e.g. Pl. 60, fig. 3, arrow; Pl. 62, fig. 1, arrow), there may have been some xylem parenchyma associated with protoxylem strands. However, this by itself does not constitute sufficient evidence for applying the term 'peripheral loop' to this plant.

Individual metaxylem tracheids range between 30 and 95 μm in transverse diameter in the first-order axis, and between 25 and 60 μm in the second-order axis. Some of these were observed with elliptical apertures (Pl. 60, fig. 6), but is unclear whether the tracheids are characterized by circular bordered pit pairs or scalariform or reticulate secondary wall thickenings. No difference in wall sculpturing has been noted between radial and tangential walls of the elements. Probable protoxylem elements, with diameters between 10 and 30 μm, were observed only in transverse section.

The region of presumed primary phloem is not well preserved in this specimen. In a few cases (Pl. 61, fig. 2, arrow **b**), small cells, approximately 30 μm in diameter, occupy positions immediately adjacent to xylem elements. It is possible that these cells were phloem conducting elements, but no distinct histological evidence, except their position, supports this interpretation. Immediately exterior to the small cells is a poorly preserved region, probably innermost cortex in part but also, perhaps, outer phloem or pericycle. In transverse section, cells of this region are very large, up to 300 μm in diameter and radially elongate. Many contain dark substances in their lumina. However, most cells are represented by isolated, radially aligned wall fragments and there is little evidence of histological zonation or a distinct boundary between vascular and cortical tissues.

Relationship between axis orders

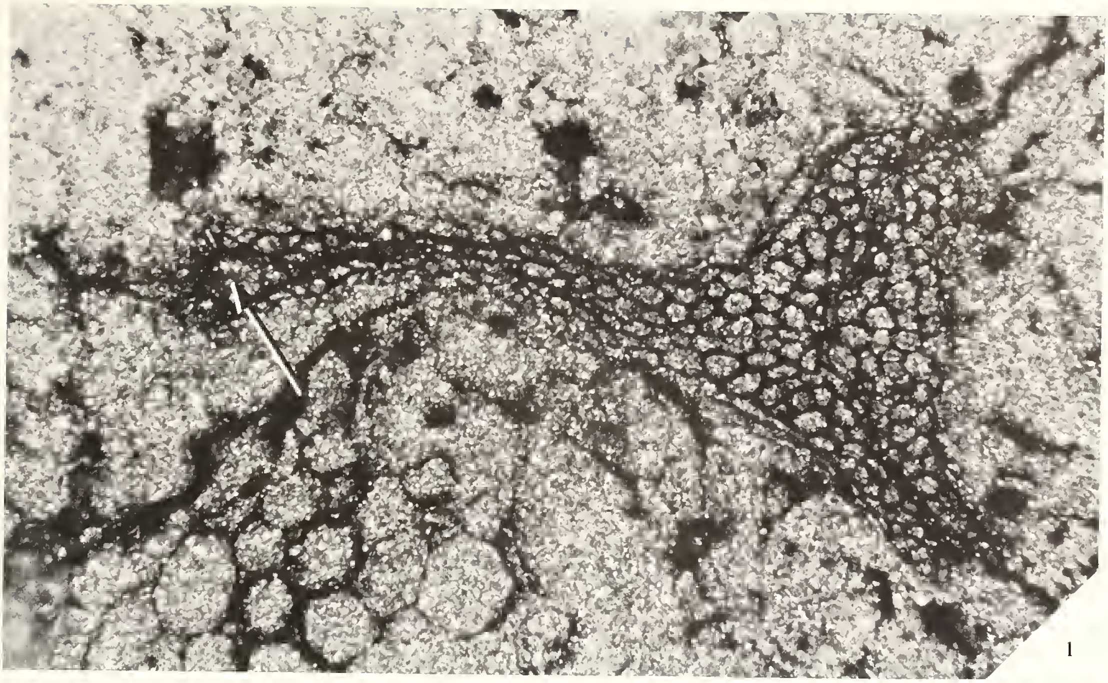
Proof of organic connection of the three axis orders can be seen in Pl. 60, figs. 1 and 4 and Pl. 61, fig. 1, where continuity of cortical tissues is evident. Traces to second-order axes were not observed to depart the primary xylem of the first-order axis. At the most proximal level of its occurrence in the specimen, the primary xylem of the preserved second-order axis is already enveloped by its own cortical tissue (Pl. 60, fig. 1). However, evidence of an additional trace to a second-order axis, incipient in the preserved region of the first-order axis, can be inferred from the marked tangential expansion of the tip of one of the primary xylem ribs (Pl. 60, fig. 1, arrow **b**). The presence of one trace at a great distance from the primary xylem of the central stele, an incipient trace at an adjacent primary xylem rib, and a third xylem rib with no associated trace suggests a helical but widely spaced $\frac{1}{3}$ 'organotaxy'.

Departure of traces from the primary xylem of the second-order axis also was not directly observed. At the most proximal level of their occurrence in the specimen, traces to the third order are found in the cortex of the second-order axis (Pl. 60, fig. 4). Distally, they occupy the central portions of independent axes (Pl. 60, fig. 5). The second-order axis produces laterally (i.e. tangentially with respect to the first-order axis) the first two traces in a sub-opposite pair. Through the course of departure, these traces divide once equally in a plane at right angles to the plane of their departure (i.e. tangentially with respect to the second-order axis). Distally, pairs of traces vascularize third-order axes which appear to be bifurcate at or near their bases (Pl. 61, fig. 1, arrow).

Successive transverse sections through more distal portions of the preserved second-order axis shows increased elongation of the abaxial primary xylem rib (Pl. 61, fig. 3). This feature is probably associated with the departure of an additional trace. It is unclear, however, whether the trace actually departs the primary xylem in the region of the preserved specimen. It may be reasonable to assume that trace departure here is associated with a division of the protoxylem strand near the tip of the elongated rib, but preservation is insufficient to determine if this really happens or not. The configuration of cortical tissues immediately adjacent to the elongated xylem rib suggests that distally this trace divides, but this also was not actually observed.

EXPLANATION OF PLATE 62

Figs. 1–3. *Reimannia aldenense* Arnold—type specimen from Erie County, New York. UMMP No. 16231. Second-order axis, transverse sections. 1, detail of primary xylem between the levels shown in Pl. 60, fig. 3 and Pl. 61, fig. 3. Arrow indicates a protoxylem strand with a poorly preserved centre (previously interpreted as a peripheral loop) probably associated with an incipient trace, × 80. 2, detail of primary xylem near the base. Arrow indicates the same protoxylem strand marked with an arrow in fig. 1, × 80. 3, detail of primary xylem near the level of Pl. 60, fig. 5, × 80.



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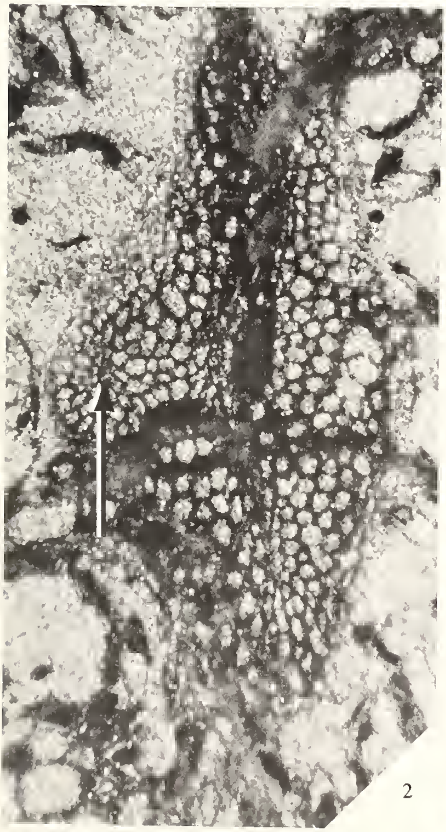

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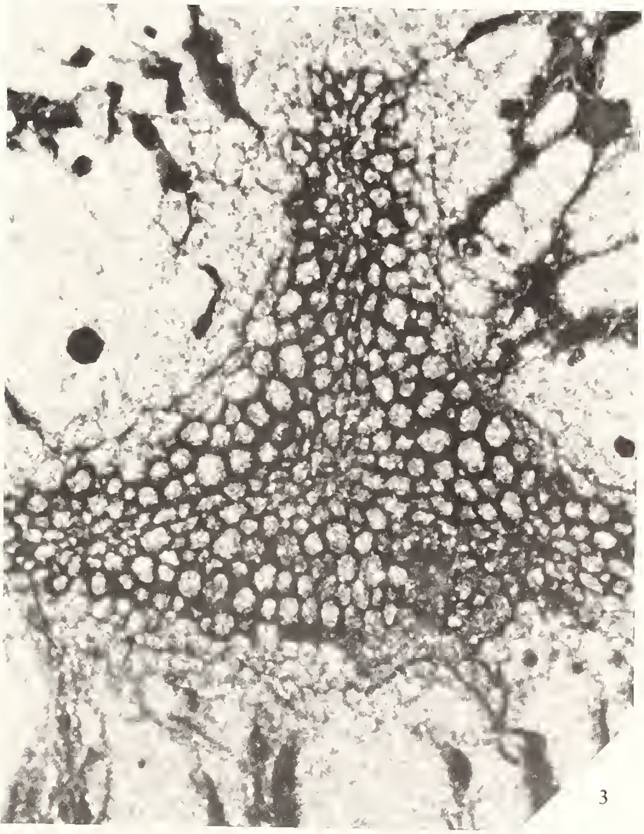


3

STEIN, *Reimannia*

Genus REIMANNIA Arnold, 1935

Amplified diagnosis. Plants, represented by permineralized axes with three orders of branching, containing primary tissues only. Vascular tissues protostelic. Primary xylem three-ribbed in first- and second-order axes, circular in transverse section in traces to the third order. Primary xylem maturation mesarch. Protoxylem strands simple, occurring near the tips or along the median planes of primary xylem ribs in the first- and second-order axes, occurring singly in the centre of the primary xylem of third-order traces. Order of trace departure in the first-order axis probably helical ($\frac{1}{3}$ 'organotaxy'). Primary xylem of second-order axis four-angled proximally, producing a sub-opposite pair of traces, becoming three-ribbed distally and probably producing a single abaxial trace. Traces to third-order axes dividing once equally in a tangential plane with respect to the parent second-order axis. Some cells surrounding the primary xylem with dark materials in their lumina. Cortex consisting of cells decreasing in size and increasing in cell wall thickness toward the periphery of axes; outermost cortex comprised of a semi-discrete tissue of hypodermal sclerenchyma. Epidermis consisting of isodiametric to radially flattened cells as seen in transverse section, containing dark materials in their lumina.

Reimannia aldenense Arnold

Amplified diagnosis. Plants as described in the generic diagnosis. First-order axis 9·5 mm in diameter at greatest extent containing primary xylem with 3 mm maximum diameter and rib width of 0·6 mm. Second-order axis 6·5 mm in diameter containing primary xylem approximately 1·3 by 0·7 mm proximally, attaining dimensions of 0·8 by 1·5 mm distally. Bases of third-order axes approximately 3 mm in diameter containing primary xylem strands 0·1 mm in diameter. Primary xylem of second-order axis often containing tangentially flattened tracheids, as observed in transverse section, along median planes of the primary xylem connecting four discrete protoxylem strands, one near the tip of each rib and one located at the centre of the xylem column. Protoxylem tracheids measuring 10 to 30 μm in diameter possibly disintegrating in incipient traces. Metaxylem tracheids outside median band from 30 to 95 μm in diameter. Cells of the inner cortex between 35 and 200 μm in diameter, isodiametric to twice or three times longer than wide. Cells of the outermost cortex elongate, usually between 30 and 80 μm in diameter. Epidermal cells ranging between 80 and 130 μm in diameter, probably isodiametric to slightly flattened, probably no more than twice longer than wide.

Holotype. Twenty-two slides and fourteen unmounted sections bearing number 16231 in the Museum of Paleontology of the University of Michigan, Ann Arbor, Michigan, U.S.A.

Locality. Spring Creek near Alden, Erie County, New York, U.S.A. Pyrite horizon in the Ledyard Shale Member, Ludlowville Formation, Hamilton Group (Givetian).

DISCUSSION

Concept of the genus

The genus *Reimannia* is monotypic, and at present, only the type specimen can be assigned without doubt to the type species, *Reimannia aldenense*. The reinvestigation of this specimen provides a much clearer concept of this taxon than has been held heretofore (for example, see Scheckler and Banks 1971*b*; Scheckler 1974; Beck 1960*b*). Significant new information includes: (1) three orders of branching in organic connection, (2) changes in configuration of the primary xylem in the second-order axis, and (3) positions of protoxylem strands in the primary xylem of first- and second-order axes. In light of the new information, the doubt expressed by Scheckler (1974) about the 'naturalness' of *Reimannia*, although not removed is at least somewhat lessened. Although clearly not one of the most completely understood of Middle Devonian plants, it is known to an extent comparable to many other stem fragment genera.

From time to time, other specimens have been assigned to *R. aldenense* based primarily upon general similarities with the three-ribbed primary xylem of the second-order axis, and the presence of an ill-defined 'peripheral loop' type of protoxylem strand (Matten 1973; Banks 1966; Wilcox 1967). To the extent I can tell from the published descriptions, none of these specimens share a sufficient number of characters with what is now known in *Reimannia* to be confidently assigned to the genus. In one case, an axis placed in *Reimannia* by Matten (1973, see his figs. 6 and 7, p. 622) is clearly not assignable to this genus. It is characterized by the presence of a pair of tangentially aligned protoxylem strands near the tip of one of the three primary xylem ribs, and is thus clearly different from the condition in the second-order axis of the type specimen. In the future, possible new specimens should be assigned to *R. aldenense* only on the basis of the new combination of characters reported here. I agree with the reasons for the establishment of *Reimanniopsis* (to include the former *Reimannia indianensis* Read and Campbell 1939) by Hoskins and Cross (1951) for the material from the New Albany Shale, and like several recent workers (Matten and Banks 1969; Beck 1960*a*), I see no compelling reason to consider *Reimannia* and *Reimanniopsis* closely related.

Systematic affinities

The combination of characters now available for *Reimannia* no longer supports a close relationship for this plant with *Iridopteris* or *Arachnoxylon* (Read 1938; Arnold 1940, 1947; Stein 1981). Instead, I suggest that *Reimannia* is clearly more similar to the permineralized axis fragment members of the Aneurophytales (Progymnospermopsida) (see Bonamo 1975, 1977; Beck 1976). Features which support this relationship include: (1) ribbed columns of primary xylem with mesarch order of maturation, (2) simple protoxylem strands located near the tip of each primary xylem rib or along the median planes of the ribs, (3) a helical order of trace departure, and (4) a general equivalence between the taxa in the organization of successive axis orders. In view of these similarities, lack of secondary tissues in *Reimannia* is not judged to be of systematic significance since variation in these tissues occurs at single levels in most plants during normal development. Additional aspects of the morphology of *Reimannia*, relevant to the proposed change in the systematic placement of this genus, merit brief consideration below.

Like other members of Arnold's Iridopteridineae, the attribution of a 'peripheral loop' to *Reimannia* was based upon very little direct evidence (for a discussion of this problem in more detail, see Stein 1981). In transverse section, I have been unable to find any evidence of a distinct parenchymatous tissue in the region of the 'loop'. Thus, Arnold's original description of this region (1935, p. 6) as 'an open area' (now filled with pyrite) is clearly a more objective representation of what is actually present (see Pl. 62, fig. 1, arrow). The unusual association of a supposed 'peripheral loop' in *Reimannia* with normal protoxylem strands at single levels in the plant, and the association of the peripheral loop with an incipient trace, has been appreciated by most authors who have considered the genus in any detail (Arnold 1935, 1940; Hoskins and Cross 1951; Leclercq 1970). Surprisingly, however, in most cases this has not lessened convictions about the applicability or the usefulness of the term as applied to this or other Devonian genera. Because there is no direct histological evidence for a specialized structure of the protoxylem in *Reimannia*, I suggest discontinuance of the term as applied to this taxon. I suggest, furthermore, that the 'open area' probably represents a developmental feature of the plant associated with trace departure, perhaps a protoxylem lacuna. These suggestions, although made independently of any taxonomic relationship for *Reimannia*, are nevertheless clearly in line with interpretations made by others of apparently identical structures observed in members of the Aneurophytales. For example, compare *Reimannia* with *Proteokalon* at an equivalent level (Scheckler and Banks 1971*b*, p. 876, fig. 8) in which a similar 'open area' is not interpreted as a peripheral loop.

A distinct band of tangentially flattened tracheids, usually one or two cells wide, as observed in transverse section, occurs at several levels in the primary xylem of the second-order axis of *Reimannia* (Pl. 62, fig. 1). This feature has been variously interpreted in *Rellimia* and *Triloboxylon*, where it also occurs, as a continuous or discontinuous median band of protoxylem (Matten and Banks 1966; Bonamo 1977) or a median band of metaxylem linking descrete protoxylem strands (Scheckler and

Banks 1971*b*). I prefer the latter interpretation not only because of the scalariform to reticulate wall sculpture of these cells reported by Scheckler and Banks, but also because in *Reimannia* (Pl. 60, fig. 3; Pl. 62, figs. 1-3) as well as in *Triloboxylon* (Scheckler and Banks 1971*b*, fig. 5) and *Rellimia* (Bonamo 1977, fig. 20), protoxylem strands appear to be clearly recognizable descrete entities. Scheckler and Banks note the intermittent occurrence of the median band of metaxylem in *Triloboxylon* but stress its possible usefulness as a taxonomic character. At present, however, I am unsure of the morphological significance or systematic importance of this feature.

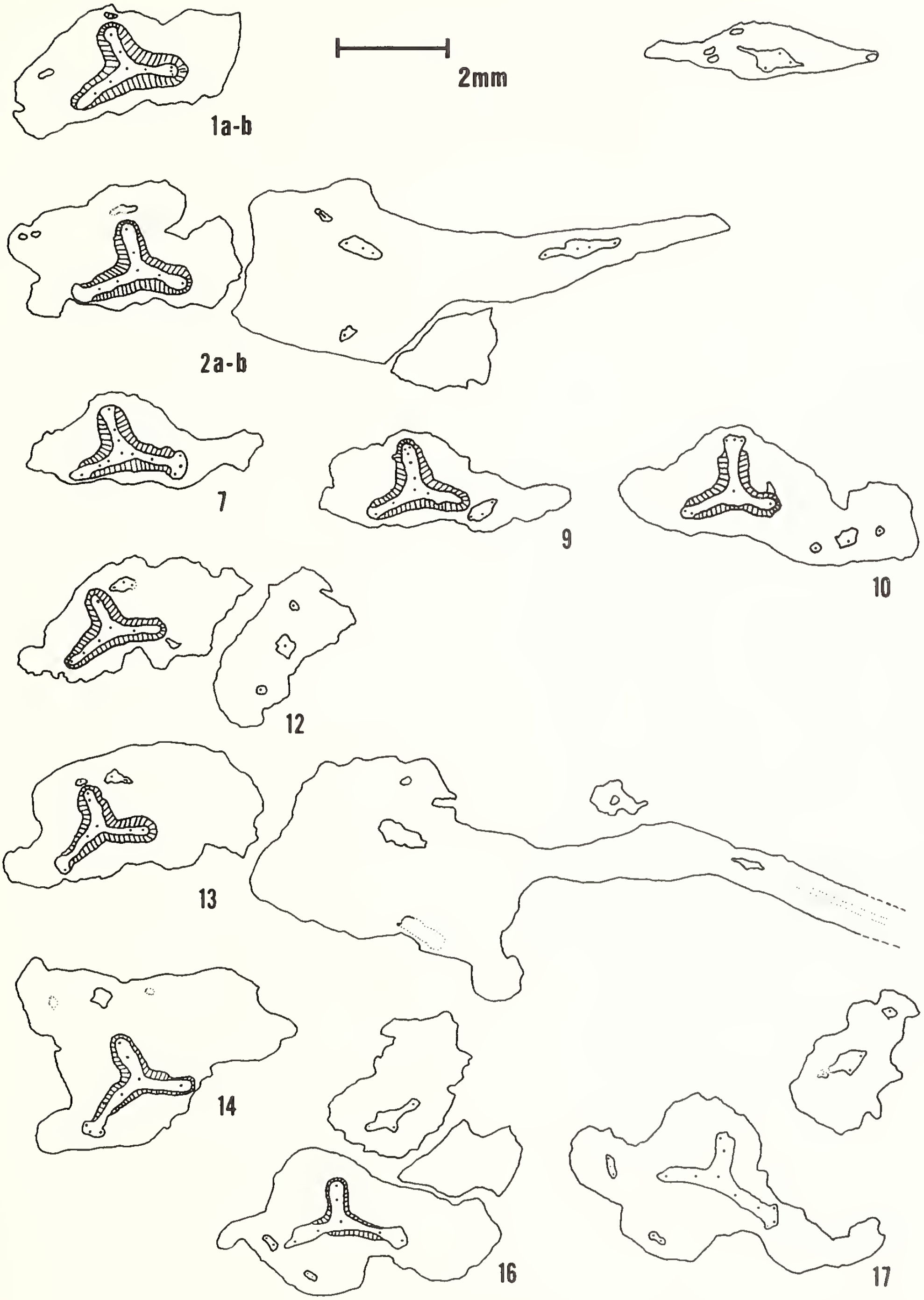
Related taxa

Reimannia aldenense resembles the published description of *Cairoa lamanekii* (Matten 1973, 1975) more than that of any other known aneurophytalean taxon. Similar features include: (1) a first-order axis ('penultimate axis' of Matten) containing a deeply three-ribbed aneurophytalean stele, (2) a trace to a second-order axis (the 'ultimate axis' of Matten) which is proximally broadly elliptical or diamond-shaped in transverse section containing protoxylem strands near the single abaxial and two lateral angles of the trace, (3) a sub-opposite pair of traces to third-order axes (the 'ultimate appendages' of Matten) at the base of the second-order axis, each elliptical in transverse section containing a single protoxylem strand, bifurcating at least once distally, and (4) similar histological features of phloem or inner cortex (including cells filled with dark materials), outer cortex, and epidermis. However, *Reimannia* differs from *Cairoa* by being larger at nearly all equivalent levels. It also lacks secondary xylem (a feature not necessarily viewed as significant), and lacks the alternating bands of parenchyma and sclerenchyma observed in *Cairoa*. Furthermore, the primary xylem of *Reimannia* becomes distinctly three-ribbed in distal portions of the second-order axis whereas in *Cairoa*, according to Matten's description, the primary xylem remains elliptical or becomes increasingly four-angled as seen in transverse section, thus *not* repeating the primary xylem configuration of the previous order. If Matten's interpretation is correct, then this feature alone could serve to distinguish the two genera. I have had the opportunity to study the type specimen of *C. lamanekii* (text-fig. 2). I am not convinced that the observed pattern of trace departure from the primary xylem of the first-order axis and the orientation of second-order axes, in organic connection with the first (text-fig. 2, sections 1*a*, *b* and 7 to 13), are necessarily explained by simple right angle bends in some second-order ('ultimate') axes as proposed by Matten (1975). Particularly disturbing is the fact that some of the laterals, those with the most clearly defined rhomboidal primary xylem (text-fig. 2, sections 1*a*, *b* and 2*a*, *b*), were observed to be reflexed (i.e. borne backwards at an angle from the first-order axis greater than 90°). Furthermore, the primary xylem of these laterals has not yet been proven to be the distal continuation of the primary xylem of the observed second-order traces. It is possible that the reflexed axes are in fact additional appendages, perhaps roots or root-like stems, attached to the base of at least some second-order axes.

Reimannia is similar in most major respects to the genus *Triloboxylon* (Matten and Banks 1966; Scheckler and Banks 1971*a*). The only differences between the two genera, at present, seem to be the four-angled configuration of primary xylem and the presence of a sub-opposite pair of traces in the basal second-order axis of *Reimannia* as opposed to a basal three-ribbed configuration in *Triloboxylon* with an apparent helical order of trace departure from the start. These differences may be insufficient to distinguish taxa, however, since considerable variation can be observed in aneurophytes under study in this laboratory.

A striking resemblance is noted between the second-order axis of *Reimannia* and the second-order 'branch' of the lower Upper Devonian genus *Proteokalon* (Scheckler and Banks 1971*b*) in the configuration of the primary xylem, the location of protoxylem strands, and in the overall size relationships of vascular tissue to cortex. The primary xylem of the first-order axis in *Proteokalon* is four-ribbed, however, and contains conspicuous metaxylem parenchyma whereas in *Reimannia*, to the extent known, metaxylem is composed of tracheids only and the vascular system is three-ribbed.

In 1973 Matten suggested that within the Aneurophytales, *Proteokalon* and *Cairoa* should be placed in a separate family since successive orders in these plants show changes in the number of primary xylem ribs. This system may not be workable, however, because variability in the



TEXT-FIG. 2. Type specimen of *Cairoa lamanekii* Matten from Greene County, New York. *Camera lucida* diagrams showing some aspects of trace departure in this specimen. Section numbers are indicated beside each drawing. The most proximal level of the specimen presented here is section 1*a*, *b*, and the most distal is section 17.

configuration of the primary xylem within single axis orders of aneurophytes is becoming evident. For example, a change in the primary xylem column from four-angled to three-ribbed has been noted in the second-order axis of *Reimannia*, and in one second-order axis of *Proteokalon*, the primary xylem has been observed to change from three-ribbed proximally to distinctly four-ribbed distally (Scheckler and Banks 1971*b*; Scheckler, pers. comm. 1978).

CONCEPT OF THE PROGYMNOSPERMOPSIDA

As presently conceived, the class Progymnospermopsida is comprised of three orders and between fifteen and twenty genera depending upon the acceptability of some assignments (Barnard and Long 1975; Bonamo 1975; Beck 1976). From the start (Beck 1960*b*), members of this group have been considered phylogenetic intermediates between the primitive vascular plants of the Lower Devonian, now placed within the Rhyniophytina and Trimerophytina of Banks (1968), and early seed plants, the oldest of which occur in sediments of late Upper Devonian age. More specifically, the Progymnospermopsida have been considered to comprise the basal portions of a single clade of vascular plants, the members sharing some, but not all, of the derived features of seed plants. To accommodate this idea, evidence for membership in the Progymnospermopsida has often been spelled out in a combination of primitive (free-sporing habit), and derived ('typically gymnospermous' secondary vascular tissues) characters (Beck 1960*b*, 1976; Bonamo 1975). In my opinion, it is permissible to define a group in this manner so long as one accepts the initial postulate that one or several members of this group were actually the *direct ancestors* of the later forms. To be sure, a postulate of direct ancestry is only one of several possible phylogenetic trees included in a 'sister group' hypothesis proposed by strict adherence to cladistic methodology (see Hennig 1979; Eldredge 1979; Eldredge and Cracraft 1980) and, as opposed to the later, not arrived at solely by analysis of characters. However, it is clearly falsifiable.* Furthermore, when repeated testing fails to falsify either postulate, the fact that direct ancestry is only one hypothesis about what actually happened, as opposed to several, is more impressive to me.

In the case of the Progymnospermopsida, I am inclined to accept as a working hypothesis the position of the group as direct ancestors of seed plants even though the present understanding of characters is insufficiently detailed to enable one to recognize natural species, or to determine which of the known taxa actually gave rise to descendent groups, or even to know how many descendent groups actually evolved from this plexus of forms. This acceptance is based primarily upon stratigraphic evidence that recognizable members of the Progymnospermopsida significantly predate the earliest occurrences of seeds, and upon the confidence that the combination of potentially independent characters comprising 'typically gymnospermous' secondary vascular tissues (as opposed to other possible or actual types of secondary tissues) was unique in occurrence in the history of vascular land plants. However, in accepting the definition of the Progymnospermopsida given above, it is important to realize that the two kinds of characters used to circumscribe the group, primitive and derived, contain distinctly different information about phylogenetic history. Thus, when considering possible phylogenetic patterns within the Progymnospermopsida, or even membership in the group, the two types of characters should not be treated as equivalent information.

In 1975 Bonamo suggested that taxa within the Progymnospermopsida should be segregated into categories in order to minimize confusion of those which represent isolated permineralized axis fragments or fragmentary compressions, with others representing 'whole' organisms more or less completely understood. I feel this approach is helpful since it emphasizes the degree to which taxa are known, and underscores the importance of evaluating the extent of morphological comparability between named entities. However, one must recognize that although some taxa are incompletely known at present, the discovery in the future of additional information about these forms may necessitate significant changes in our view about their systematic importance. Thus, I would not agree with Bonamo (1977) if she concluded that the concept of a taxon-like *Triloboxylon ashlandicum*, formerly known from details of internal anatomy and, to a limited extent, branching patterns, should not be extended to encompass structures found in organic connection, such as the sporangial complexes proposed by Scheckler (1975). This would be a fundamental contradiction of the general application of botanical scientific nomenclature (see Schopf 1978). If, on the other hand, Bonamo meant to say that proof of organic connection in a single case should not be considered as proof of a similar connection in all other cases within the genus *Triloboxylon*, then I would certainly agree.

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* One can disprove the hypothesis that one taxon is ancestral to another by discovering clear advancements in the proposed ancestor which are not shared by the proposed descendent (i.e. 'autapomorphous characters' in the terminology of Hennig 1979).

In the categorization of taxa within the Progymnospermopsida, Bonamo (1975) suggested that only those taxa showing positive evidence of a free-sporing habit combined with 'typically gymnospermous' secondary vascular tissues, the combination of characters originally cited in the establishment of the group, can be considered bona fide members. She used the categories ('incertae sedis (anatomy)' and 'incertae sedis (morphology)' for less complete, but presumably related, forms known primarily on the basis of internal anatomy alone or external morphology alone respectively. This approach represents an attempt to be as rigorous as possible in the definition of the Progymnospermopsida in order to exclude disparate elements which, on the basis of incomplete evidence, might otherwise be assigned to the group. However, a weakness in this scheme, in my opinion, lies in the fact that primary consideration for membership in the Progymnospermopsida then rests on only two of many potentially useful characters. Much recent work (Bonamo and Banks 1967; Leclercq and Bonamo 1971; Bonamo 1977; Beck 1971, 1979; Serlin and Banks 1978; Scheckler and Banks 1971*a*, *b*; Scheckler 1975, to name a few examples) has shown that other features of progymnosperms, such as the architecture of the primary vascular system or the morphology of sporangial complexes, may be equally useful in determining membership in this group. In this report, for example, I have presented what I consider to be good evidence for placement of *Reimannia aldenense* within the Aneurophytales of the Progymnospermopsida even though the type specimen lacks evidence of either original defining character.

Another problem is that, as noted above, the two original diagnostic characters, one primitive and the other derived at this level of analysis, do not contain equivalent phylogenetic information. Therefore, in terms of systematic significance, the failure of certain taxa positively to demonstrate one of the characters should not be interpreted in the same way as the failure of other taxa to demonstrate the presence of the other. Clearly, the derived characters are more important. For example, if one accepts that 'typically gymnospermous' secondary tissues arose only once, then the presence of this derived character in incompletely understood forms such as *Triloboxylon*, *Proteokalon*, and *Cairoa* is sufficient to ally them with the Progymnospermopsida. Furthermore, if one considers the stratigraphic occurrences of these forms, it becomes relatively certain that they do in fact represent members of the Progymnospermopsida even though the specimens fail to demonstrate a free-sporing habit. On the other hand, the primitive character contains far less information. Under no circumstance would one feel justified in placing a taxon within the Progymnospermopsida in the absence of any knowledge of internal structure simply on evidence of 'pteridophytic reproduction'.

For these reasons, I suggest the use of more descriptive categories within the Progymnospermopsida not tied to the demonstratable presence of specific primitive or derived characters, but emphasizing instead only the nature of the evidence collected for each taxon. Requirements for membership in the group, in my opinion, should be treated as an entirely separate issue. For each taxon, this decision should be based on all available evidence and, of course, is subject to close scrutiny and debate. Table 1 presents my view of the Aneurophytales of the Progymnospermopsida, the group to which *R. aldenense* is now assigned. In this list, primary emphasis is placed on the type of information required to recognize taxa from the fossil record.

Perhaps the best-known aneurophytalean taxon, from the standpoint of understanding the whole plant, is *Tetraxylopteris schmidtii* (Beck 1957; Scheckler and Banks 1971*a*; Bonamo and Banks 1967). Not only are fertile structures known in considerable detail, but they are understood in the context of several orders of decussate branching which in turn is correlated with information on primary

TABLE 1. A list of probable members of the Aneurophytales (Progymnospermopsida) according to the nature of the evidence for each

Genera recognized primarily from internal structure	Genera recognized from either internal anatomy or external morphology	Genera recognized primarily from external morphology
*Stauroxylon**	*Tetraxylopteris*†*	*Rellimia*†*
Triloboxylon		*Aneurophyton*†*
ashlandicum†*		(*Eospermatopteris*)
*arnoldii**		
*Proteokalon**		
*Cairoa**		
Reimannia		

* Secondary tissues reported.
† Fertile regions reported.

vascular architecture. Although placed in the centre category in Table 1, this does not mean that the plant is completely understood. Serious unresolved questions remain concerning the proposed helical versus decussate organization of the main axis of the plant (Beck 1957; Banks 1970; Bonamo, pers. comm. 1979), as well as the relationship of aerial axes to rooting structures, and the overall stature of the plant. However, the plant may be reliably identified either from internal anatomy or from external morphology.

Rellimia (Kräusel and Weyland 1933; Leclercq and Bonamo 1971, 1973; Bonamo 1977) and *Aneurophyton* (Kräusel and Weyland 1923, 1926, 1929; Leclercq 1940; Serlin and Banks 1978) are genera whose sporangium-bearing complexes are known in detail along with information on branching patterns. In addition, a certain amount of data exists on the anatomy of these genera and suggestions have been made (Scheckler and Banks 1971*a*, *b*; Bonamo 1977; Serlin and Banks 1978) on how to separate the taxa on this basis (e.g. amount of primary xylem ribbing, location, and number of protoxylem strands). However, the vascular architecture of either plant, particularly trace departure and changes in vascular organization from one axis order to the next, remains at present very incompletely understood. Thus, I maintain that information on the anatomy of these genera is insufficient to enable one to distinguish them from each other or from several other forms known only from permineralizations. It is characteristics of external morphology alone which make the taxa recognizable.

Eospermatopteris (Goldring 1924), large sandstone casts found with compression material thought to resemble *Aneurophyton*, presents a very weak case for its inclusion in the Progymnospermopsida. We are now aware of several kinds of Middle Devonian plants, besides presumed ancestors of seed plants, which attained arborescent stature.

In contrast to above, *Triloboxylon ashlandicum* (Matten and Banks 1966; Scheckler and Banks 1971*a*, *b*; Scheckler 1975, 1976), *Triloboxylon arnoldii* (Arnold 1940; Scheckler and Banks 1971*a*, *b*; Matten 1974), *Cairoa lamanekii* (Matten 1973), *Proteokalon petryi* (Scheckler and Banks 1971*b*), *Stauroxylon beckii* (Galtier 1970), and *Reimannia aldenense* are known mostly from fragmentary permineralized specimens showing only evidence of internal anatomy. These should be considered to be axis fragment form genera, not equivalent, and only partially comparable to *Tetraxylopteris*, *Rellimia*, and *Aneurophyton*. When compared among themselves, and with equivalent information from the other forms, there is evidence of considerable variability in the organization of primary vascular tissues which is in turn suggestive of a considerable diversity within this group. However, the magnitude of variation within single taxa has not yet been established and it is therefore difficult to decide on the importance of what has been observed to date.

Thus, with respect to the Aneurophytales as a whole, two lines of evidence have been accumulating which for the most part have offered little in the way of directly comparable evidence. From compressions, we know something about their overall morphology and are beginning to understand some of the characters which might serve to further delimit the group in a more or less biological way. From the study of internal structure, we are accumulating evidence of diversity but, as yet, the meaning of this kind of evidence is less evident.

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THE TRILOBITE GENUS *EOHARPES* FROM THE ORDOVICIAN OF BRITTANY AND PORTUGAL

by MICHAEL ROMANO *and* JEAN-LOUIS HENRY

ABSTRACT. Eoharpid trilobites from the Ordovician of Brittany and Portugal are revised. *Eoharpes guichenensis* Henry and Philippot of Llandeilo age from Brittany is redescribed on the basis of new material and *E. macaoensis* sp. nov. of probable Caradoc age from central Portugal is described. The broadly contemporaneous Armorican species *E. guichenensis* and *E. cristatus* Romano from north Portugal enforces the strong faunal link between the Martigné-Ferchaud synclinorium south of Rennes and the Valongo area during the Llandeilo.

HARPID trilobites are an uncommon element of the Ordovician trilobite faunas of Brittany and Portugal and indeed, as pointed out by Whittington (1949), the group never appears to be numerically abundant even though they persisted over a long period of time and are widely distributed. In the Ordovician of Brittany and Portugal the group is represented by the genus *Eoharpes* Raymond and occurs in beds of Llandeilo age, probably reaching up to the Caradoc in Mação, central Portugal. In Brittany, *E. guichenensis* Henry and Philippot has only been recorded from the Martigné-Ferchaud synclinorium at Traveusot-en-Guichen, south of Rennes (text-fig. 1), where it occurs in the upper part of the Traveusot Formation corresponding to the top of the *Placoparia* (*Coplacoparia*) *tournemini* biozone and base of the *P.* (*C.*) *borni* biozone. In Portugal *E. cristatus* Romano is known from Valongo (upper part of Valongo Formation) and possibly Bougado at a similar level to that of *E. guichenensis* while at Mação *E. macaoensis* sp. nov. is probably of Caradoc age and occurs in the 'Schistes à *Orthis Berthoisi*' (Delgado 1908, p. 80).

E. guichenensis has previously been described by Chauvel and Henry (1966) and Henry and Philippot (1968) but the discovery of new material has allowed a more detailed description to be given here. The Portuguese material has received only brief attention in the past. Delgado (1908) recorded *Harpes* cf. *primus* Barrande and *Harpes* sp. n. from Bougado and in the faunal lists from the 'Bassin de Tage' (Mação-Amendoa region) he recorded *Harpes* cf. *Doranni* Portlock and *Harpes* cf. *Flanaganni* Portlock. The only recent work on Portuguese harpids was by Romano (1975) who described a new species, *E. cristatus*, from the Valongo area.

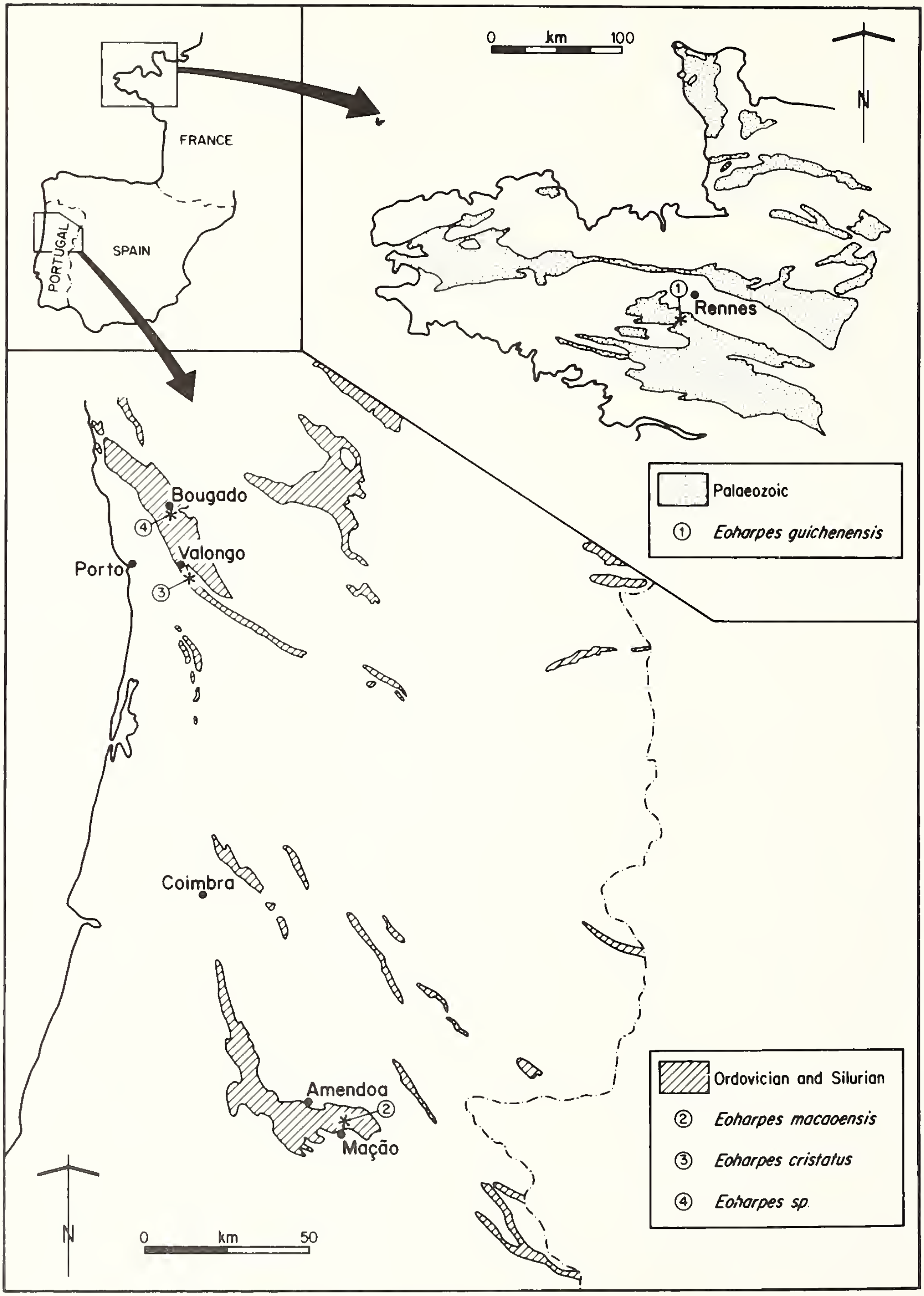
The material described and mentioned in this paper is deposited in the collections of the Geological Institute of Rennes University (IGR), Serviços Geológicos of Lisbon (S.G. and M. Romano Collection), and British Museum (Natural History) (BM In).

SYSTEMATIC PALAEONTOLOGY

General remarks. In the classification of the class *Trilobita* Harrington *et al.* (*in* Moore 1959) recognized within the suborder Harpina, three families: Harpidae, Harpididae, and Entomaspididae. Some time ago Dr. J. Miller kindly brought to our attention the fact that the name Harpidae had been used previously for a gastropod family. Owen and Bruton (1980, p. 21) have recently reviewed the situation regarding the status of Harpidae following the discussions in the *Bulletin of Zoological Nomenclature* (Beu 1971; Cernohorsky 1972; Rheder 1972, 1973). Until a ruling is made by the Commission on Zoological Nomenclature the name Harpidae is used here.

The terminology adopted is that of Whittington (1949, 1950) with the following addition. 'Alar ridge' is used for the ridge bounding the abaxial part of the ala running from the axial furrow towards the posterior border furrow.

[Palaeontology, Vol. 25, Part 3, 1982, pp. 623–633, pl. 63.]



TEXT-FIG. 1. Geographical distribution of *Eoharpes* in Brittany and Portugal showing localities mentioned in the text.

Suborder HARPINA Whittington, 1959
Family HARPIDAE Hawle and Corda, 1847
Genus EOHARPES Raymond, 1905

Type species. Harpes primus Barrande, 1856.

Diagnosis. After Whittington 1949, 1950, and *in* Harrington 1959, and incorporating our modifications: cephalon subcircular in outline, convex. Glabella gently convex, highest point at midline of occipital ring, anteriorly depressed below the cheek lobes; basal glabellar lobes small. Eye tubercles small, eye ridges may or may not be present. Alae sub-semicircular, flattened, weakly defined, and depressed below level of cheek lobes. Girder extending to tips of prolongations. External and internal surface of glabella and cheek lobe may show ornament. Cheek-roll prolongation broad, almost parallel sides, with bluntly rounded tip. Brim flat, laterally sloping gently downwards, anteriorly raised dorsally in a low fold. Pits of medium size, irregularly spaced. Hypostoma pear-shaped in outline, with broad anterior and posterior borders. Middle body oval in outline, without middle furrow. Thorax with twelve to fifteen segments, width rapidly reduced in the posterior half. Rachis moderately convex. Pleurae of characteristic harpid form, the outer parts bent vertically down. Pygidium small, outline transverse, three segments only clearly indicated.

Eoharpes guichenensis Henry and Philippot 1968

Plate 63, figs. 7–9

1965 *Eoharpes* sp.; Henry, p. 207.
1966 *Eoharpes* sp. indet.; Chauvel and Henry, pp. 64–66, fig. 1.
1968 *Eoharpes guichenensis* now. sp.; Henry and Philippot, pp. 2187–2189, pl. 1, figs. 1–3.
1980 *Eoharpes guichenensis*; Henry, pp. 39–42, text-fig. 9; pl. 2, figs. 1–4.

Diagnosis. A species of *Eoharpes* with the following characteristics: cephalon oval in outline; glabella convex (trans.), elongated, narrow anteriorly, and covered with fine reticulation; only S1 furrows visible. Cheek lobes strongly raised with anastomising genal caecae very apparent on external mould. Eye ridges very distinct on external mould, running from axial furrows level with anterior quarter of glabella length and directed obliquely backwards; eye tubercles level with mid-length of glabella, at equal distance from axial furrows and internal border of fringe. Lower lamella of fringe inclined downwards, with a maximum of six to seven pits between girder and cephalic margin.

Type and figured material. Holotype: IGR 2, internal mould of incomplete cephalon, figured by Henry and Philippot (1968, pl. 1, figs. 1–3). Paratype: IGR 1, figured by Chauvel and Henry (1966, fig. 1*a*, *b*). IGR 6 (Pl. 63, fig. 9). IGR 2340 (Pl. 63, figs. 7, 8).

Other material. IGR 3, 5, 7, 2240, 2242, 2464, 2513.

Horizon and locality. Type and other material from upper part of Traveusot Formation, Traveusot en Guichen, Ille-et-Vilaine, Brittany; Llandeilo age.

Description. The discovery, by Dr. J. Chauvel, of a remarkably well-preserved and nearly complete cephalon (IGR 6, internal and external moulds) has allowed the following detailed description.

Cephalon oval in outline. Glabella narrow, rounded, and depressed anteriorly; limited by wide, deep axial furrows and carries short, faint S1 furrows (only ones visible) orientated obliquely towards posterior. L1 lobes more or less rectangular, projecting laterally beyond sides of glabella. Distal parts of occipital furrow are deep, median portion forms shallow transverse depression. On right side of glabella along axial furrows are oval impressions, smooth and poorly defined (? muscle attachment areas). Glabella covered with dense reticulation formed of small anastomizing ridges. Alae semicircular in outline and delimited on outside by two thick branches of the genal caecae (alar ridges), smooth central zone of low relief. Pitted region in front of pre-glabellar furrow is depressed and cresent-shaped in outline. Cheek lobes strongly raised in relation to fringe, with eye tubercle connected to axial furrow by eye ridge. A second ridge runs from tubercle to internal border of fringe where it disappears. Cheek lobes covered with closely spaced and anastomizing radiating ridges (genal caecae) between which are small cavities with broadly triangular or rectangular shape. Genal caecae arranged in four bundles, symmetrical in pairs; the two anterior bundles essentially formed by numerous ridges radiating from eye and genal ridges, posterior pair originate from alar ridges. At ends of occipital ring genal caecae seem to pass imperceptibly into dense reticulation as seen on glabella. On internal moulds genal ridges appear to cut genal caecae. But on external mould of IGR 6 (Pl. 63, fig. 9) this impression is due to a difference in orientation of genal ridge compared with radiating ridges. Genal caecae much more apparent on external mould than internal mould of same specimen.

Fringe extensively perforated; width exterior to girder remaining constant except near posterior of prolongations. Pits more or less circular and randomly disposed although up to three to four sometimes aligned and clearly coalesced; pits all approximately same size (150–200 μ) except those of outermost arc on upper lamella which are slightly smaller. Between outer arc and margin of cephalon is a narrow external rim. Lower lamella contains a relatively wide, very deep girder which is marked on upper lamella by a small, smooth ridge bounded internally by large pits arranged in a curve parallel to girder. Beyond girder, on cheek roll, pits of smaller dimension appear again; laterally they are less numerous, but become more abundant anteriorly approaching preglabellar furrow. A small cephalon, with a total length of about 2 mm, was discovered in a nodule from Traveusot. Among the features of the meraspis stage of unknown degree are the developed external rim, strongly inflated cheek lobes, and the absence of S1 furrows.

Hypostoma and pygidium unknown.

Discussion. As noted earlier (Chauvel and Henry 1966; Henry and Philippot 1967), *E. guichenensis* is close to *E. primus* (Barrande 1856) and *E. benignensis* (Barrande 1872), Bohemian species which appear in the Šárka Formation (Llanvirn) and Dobrotivá Formation (Llandeilo) respectively. From the fringe pits *E. guichenensis* closely resembles *E. primus*, but is distinguished by the inclined lower lamella, the shape of the L1 lobes and the glabella which is more elongate and narrower anteriorly, the pronounced convexity of the cheeks, the more anteriorly placed eye tubercles, and the eye ridges orientated obliquely towards the genal angles. These distinctive characters are also seen in *E. benignensis*, but the pits on the fringe are here large and more numerous than in *E. guichenensis* (see Whittington 1949). For a comparison with *E. macaoensis* sp. nov. and *E. cristatus* Romano see under the discussion of those species. The assigning of the genus *Eoharpes* to the badly preserved example figured by R. and E. Richter (1954, pl. 1, fig. 5) seems debatable; the eleven thoracic segments is not characteristic of the genus as they appear to vary from twelve to fifteen (Whittington 1949, p. 223).

Eoharpes macaoensis sp. nov.

Plate 63, figs. 1–6

?1908 *Harpes* cf. *Flanaganni* Portlock; Delgado, p. 80.
?1908 *Harpes* cf. *Doranni* Portlock; Delgado, p. 80.

Diagnosis. A species of *Eoharpes* with the following characteristics: glabella nearly parallel sided and covered with fine reticulation. Prominent alar ridges round outside of alae; genal caecae radiate out

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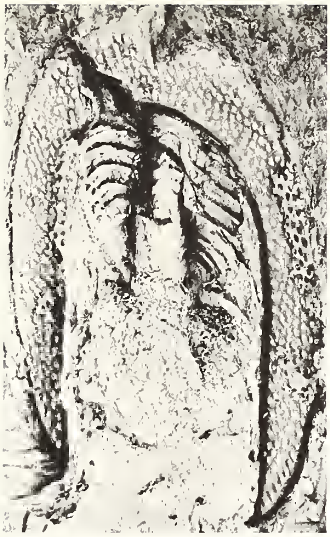
EXPLANATION OF PLATE 63

Figs. 1–6. *Eoharpes macaoensis* sp. nov. All specimens from 500 m N. 52° E. of the village of Pereiro, Mação, central Portugal. 'Schistes à *Orthis Berthoisi*', probably Caradoc. 1, incomplete cephalon, paratype, M. Romano Collection 6, internal mould, dorsal view, × 3. 2, cephalon, paratype, M. Romano Collection 8, latex cast, dorsal view, × 3. 3, 4, incomplete fringe, paratype, M. Romano Collection 7, latex cast, dorsal view, × 3 and approx. × 8·5 respectively. 5, 6, cephalon, holotype, M. Romano Collection 4, latex cast, dorsal view, 6, × 3; 5 (detail of 6), showing ornament of glabella and cheeks, × 7·5

Figs. 7–9. *Eoharpes guichenensis* Henry and Philippot, 1968. All specimens from Traveusot en Guichen, Ille-et-Vilaine, Brittany. Upper part of Traveusot Formation; top of *Placoparia* (*Coplacoparia*) *tournemini* biozone and base of *Placoparia* (*Coplacoparia*) *borni* biozone, Llandeilo. 7, 8, cephalon, IGR 2340, oblique lateral and right lateral view, × 6 approx. 9, detail of cephalon IGR 6, showing ornament of glabella and cheeks, latex cast, dorsal view, × 8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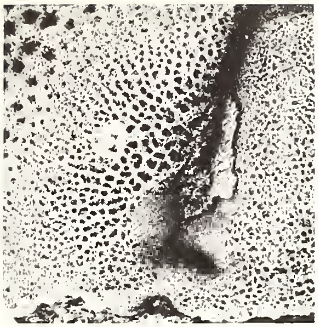
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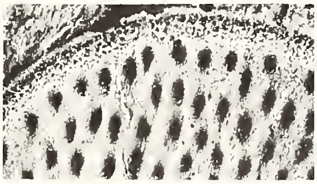
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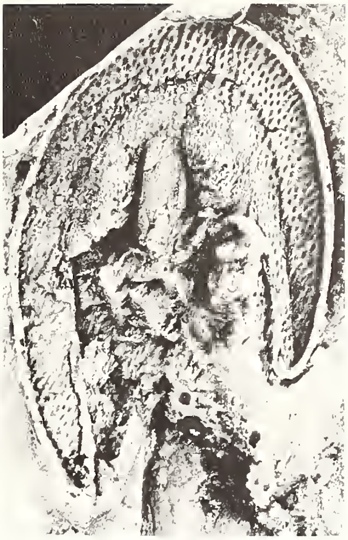
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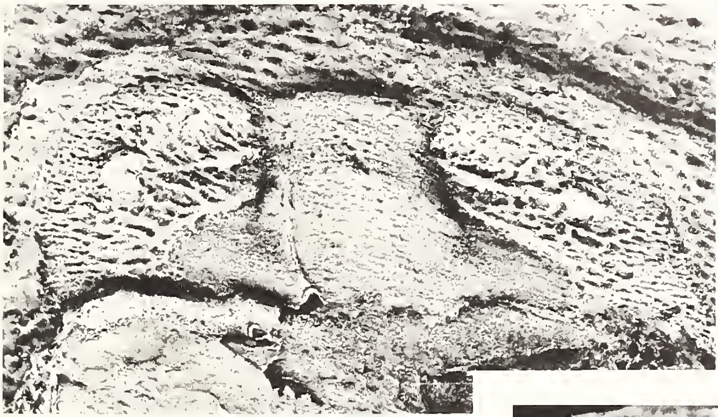
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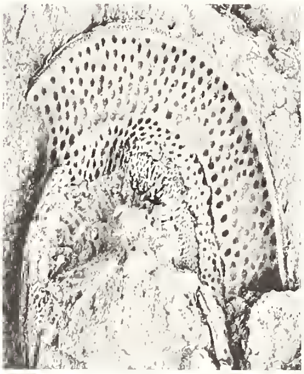
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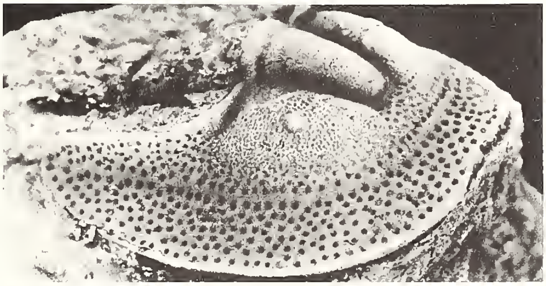
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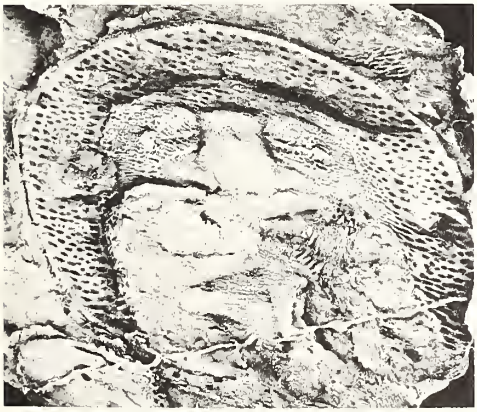
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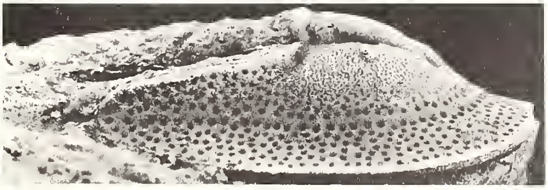
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ROMANO and HENRY, *Eoharpes*

from posterolateral corners of glabella, genal ridge absent. Approximately eighty-five pits forming outermost arc on brim where pits are slightly larger and more regular than on rest of fringe. External rim covered with fine, densely spaced tubercles which merge into a delicate reticulate pattern.

Type and figured material. Holotype: M. Romano Collection 4, external mould of nearly complete cephalon (Pl. 63, figs. 5, 6). Paratypes: M. Romano Collection 6, internal mould of incomplete cephalon (Pl. 63, fig. 1). M. Romano Collection 8, external mould of nearly complete cephalon (Pl. 63, fig. 2). M. Romano Collection 7, external mould of lower lamella (Pl. 63, figs. 3, 4).

Other material. M. Romano Collection 9, internal mould of nearly complete cephalon. M. Romano Collection 10, fragment of fringe.

Horizon and locality. All material from 500 m N. 52° E. from the village of Pereiro, Mação, central Portugal. Probably Caradoc age.

Description. Cephalon horseshoe-shaped in outline with posterolateral margins of fringe slightly incurved. Deformed material shows length to width ratios of cephalon which vary from 1:0·7 to 1:1·3. Genal prolongations extend backwards beyond posterior border for just under half the total length of cephalon. Glabella relatively narrow, under half the length of cephalon (excluding prolongation) and under one-fifth the width along posterior margin. Glabella gently convex dorsally lying below highest part of cheek lobes and sloping forwards anteriorly. Sides of glabella converge gently forwards and are evenly rounded anteriorly. Axial furrows well marked laterally but shallow anterior to glabella. S1 furrows do not appear to be present. Occipital ring delimited laterally by deep occipital furrow which fades medianly to very faint transverse depression. Surface of glabella covered with subdued reticulate ornament (visible on external and internal moulds); on holotype the reticulation has crude transverse alignment, probably the result of deformation. Semicircular-alae present adjacent to posterior third of glabella. Alae are smooth, lie below level of surrounding cheek lobe, and are delimited on outside by prominent alar ridge which runs from axial furrow and dies out before posterior border furrow. On the holotype genal caecae just cross alar ridge and come to lie on outer part of alae. Very faint alar furrow occasionally developed but normally alae delimited only by change in slope formed by ridge adjacent to flat surface of alae. Preglabellar field lying between anterior margin of glabella and girder is covered with prominent pits which grade rapidly into typical ornament on cheek lobes; anteriorly this field has uninterrupted connection with fringe pits. Cheek lobes convex, standing above glabella and sloping down steeply to fringe. Highest part occurs just anterior to mid-line (exsag.) which approximately coincides with position of eye tubercle. Eye tubercles relatively large and situated about middle (trans.) of cheek lobes. Prominent (on external mould) eye ridge runs from eye tubercle inwards and slightly forwards to axial furrow where it is best developed. Surface of cheek lobes covered with pattern of radiating and anastomizing ridges (genal caecae); furrows between ridges formed of irregular-shaped pits. Genal caecae clearly visible on external and internal moulds and radiate out from area which, when ridges traced backwards across alae, appear to originate from posterolateral part of glabella. Genal caecae decrease in width and increase in number (from ten to over thirty) from alae towards fringe by irregular branching. Relationship between genal caecae, eye ridge, and alar ridge not clear; genal ridges not definitely identified. Just in front of posterior border, where alar ridge dies out, genal caecae decrease in size and take on the more subdued ornament of glabella. Posterior border furrows deepest adaxially and die out laterally; posterior borders short (exsag.) and convex dorsally.

Fringe consists of wide brim, gently sloping outwards, and narrow cheek roll which declines steeply outwards. Deep, well-marked girder extends to tip of prolongation. More or less circular pits, relatively large and although generally randomly arranged outer and inner arcs of brim are more regular. Maximum of eighty-five pits in outer arc and approximately seventy in inner arc; six to seven pits across width of brim anteriorly. On upper lamella, site of girder marked by faint ridge with even arc of large pits external to it. Wide, convex external rim with marginal suture. Lower and upper rims covered with fine, densely spaced tubercles which merge to give delicate reticulate pattern. To a lesser extent, especially on lower lamella, this ornament continues on to fringe where tubercles encroach on outer slopes of fringe pits.

Thorax imperfectly known. One specimen shows five thoracic segments impressed through from below; they appear to be of typical harpid type.

Hypostoma and pygidium not known.

Discussion. E. macaoensis sp. nov. differs from *E. primus* in having a more pronounced pattern of radiating and anastomizing genal caecae, the eye tubercles situated further back, more clearly defined alar ridges, and the ornament of fine tubercles on the rim. *E. benignensis* has a relatively wider brim with a greater number of pits across the width; also the cheek lobes of the Bohemian species are considerably more inflated. The differences between *E. macaoensis* and *E. guichenensis* are less marked than with the Bohemian species but the absence of the genal ridge, slightly larger and more regular pits in the external arc of the brim, and the ornament on the external rim of the Portuguese species serve to distinguish it from the French species. *E. cristatus* from north Portugal does not possess eye ridges, the pattern of ridges on the cheek lobe is less distinct than in *E. macaoensis* and the ridge on the posterolateral part of the prolongation is absent in the species from Mação.

Eoharpes cristatus Romano 1975

1975 *Eoharpes cristatus* sp. nov.; Romano, pp. 28–32, pl. A, figs. 1–4.

Diagnosis (supplementary to that of Romano 1975, p. 28). A species of *Eoharpes* with the following characteristics: cephalon of horseshoe outline, glabella apparently smooth and with faint S1 furrows. Cheek lobes convex, with anastomizing, radiating genal caecae visible on internal and external moulds. Eye tubercles lie just anterior to mid-length of glabella; eye ridges absent. Approximately eighty-two pits around external arc and six to seven pits across anterior width of brim. Concentric ridge lying on upper lamella internal to outermost arc of pits on posterior part of prolongation of brim.

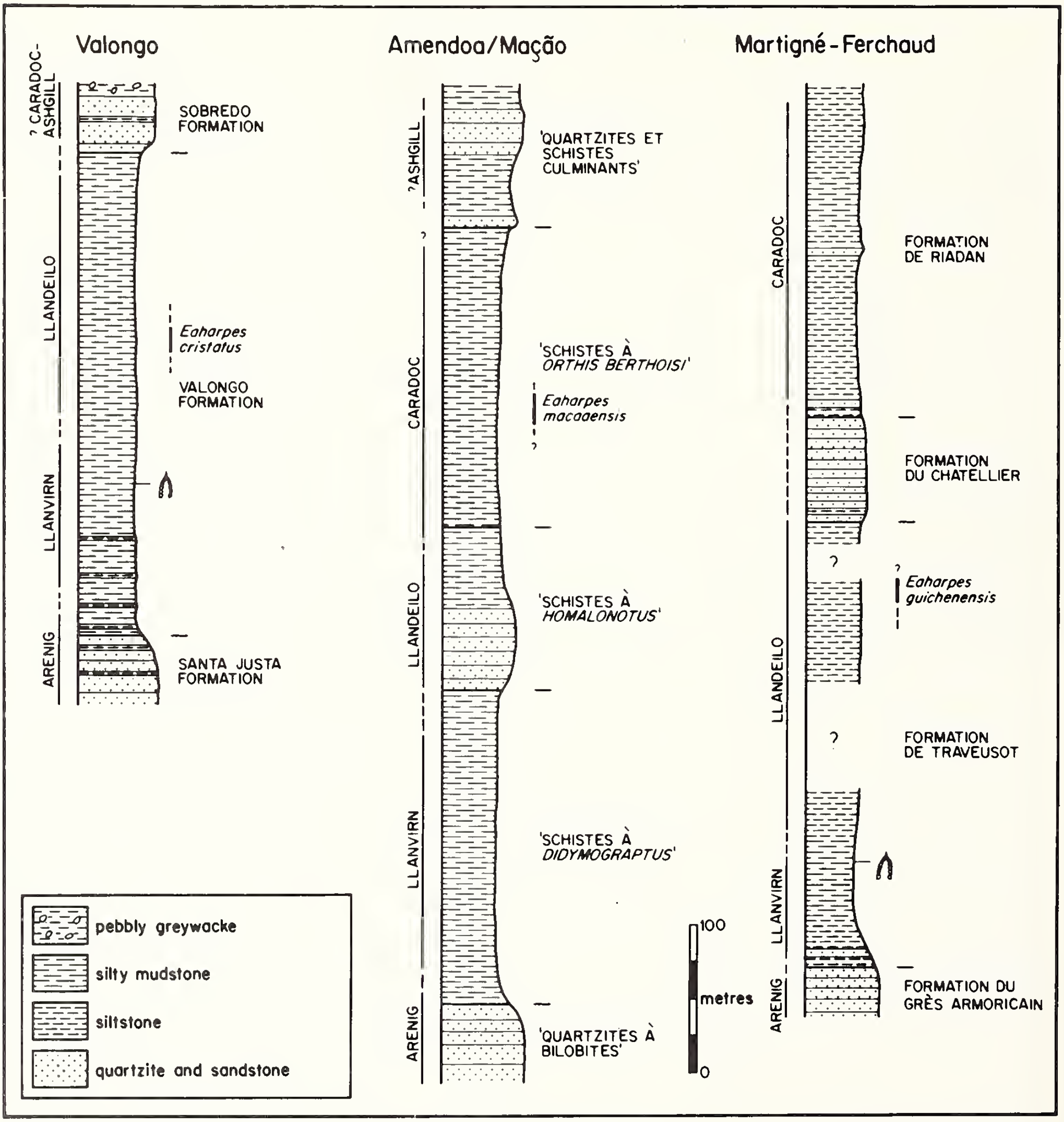
Type material. Holotype: M. Romano Collection 1, internal and corresponding external mould of nearly complete distorted cephalon.

Horizon and locality. Valongo Formation; locality A5/6, approximately 100 m above the horizon with graptolites of the *Didymograptus murchisoni* zone. Llandeilo age. Road section, east of the road, near Beloi, 5·5 km SSE. of Valongo.

Discussion. When *E. cristatus* was first described the comparison with *E. guichenensis* was based on the French material available at that time (Chauvel and Henry 1966; Henry and Philippot 1968). Since then the additional specimen discovered by Dr. J. Chauvel has allowed some further comments to be made. The major features separating the two species are the absence of the eye ridge and genal ridge in *E. cristatus*, the slightly larger pits in the outermost arc of the brim in *E. cristatus*, and the lack of the fine ridge at the posterolateral part of the prolongation in *E. guichenensis*. The difference between the two species mentioned by Romano (1975, p. 31) concerning the apparent absence of genal caecae in the French species is now no longer valid.

VERTICAL RANGE AND LATERAL DISTRIBUTION OF SPECIES OF *EOHARPES* IN THE ORDOVICIAN OF BRITTANY AND PORTUGAL

In the Traveusot Formation of the Martigné-Ferchaud synclinorium south of Rennes *E. guichenensis* occurs approximately 190 m above *Didymograptus murchisoni* Zone graptolites although the exact horizon is difficult to determine. It is found with a rich trilobite assemblage corresponding to the top of the biozone of *Placoparia* (*Coplacoparia*) *tournemini* and base of the *P.* (*C.*) *borni* biozone of Llandeilo age (Henry and Clarkson 1975). The genus has not been recorded elsewhere in Brittany. In Portugal eoharpids have been found at Bougado, Valongo, and Mação. Delgado (1908, pp. 100, 107) recorded a trilobite assemblage including *Harpes* cf. *primus* and *Harpes* sp. n. from 2000 m N. 37° W. of the trigonometrical point of Bougado, which lies approximately 18 km NNE. of Porto (text-fig. 1). The harpids occur within Delgado's 'Schists à *Didymograptus*'. In reinvestigating the Bougado area, Teixeira (1957, p. 451, fig. 1) listed *Harpes* sp. from the 'Xisto argilosos Ordoviciano' which he regarded as Llandeilo in age. More recently Romano (1975, p. 28) noted the discrepancy in dating parts of the Bougado sequence and concluded that 'some doubt must remain as to their [harpids] true age'. The Bougado harpid specimens listed by Delgado have now been traced in the collections of the Serviços Geológicos in Lisbon where the labels state that they were found 2000 m N. 20° W. of Bougado trigonometrical point. From Teixeira's map of the area (op. cit.) it would appear as though the map reference given in Delgado (1908, p. 100; i.e. 2000 m N. 37° W.) is more likely to be correct since this occurs near the western limit of Teixeira's 'Xisto argilosos' of Llandeilo age; the map reference given on the specimens in the Serviços Geológicos plots out in the 'Grauvaques e xistos gotlandianos'. While there still may be some doubt as to the true locality from which the specimens were collected, the age of the harpids may be resolved. In the collection of the Serviços Geológicos are three slabs yielding placopariid trilobites from the same locality as the harpids. These placopariids



TEXT-FIG. 2. Generalized lithological sections in the Ordovician of Valongo, Amendoa-Mação and the Martigné-Ferchaud synclinorium showing the stratigraphic position of the species of *Eoharpes*. The position of the last Llanvirn *Didymograptus* is also shown.

may definitely be identified as *P.* (*C.*) *tournemini* which is of Llandeilo age in Iberia (Hammann 1971; Romano 1975), and the Armorican Massif (Henry and Clarkson 1975), and confirms the Llandeilo age suggested by Teixeira.

The specimen from Bougado identified by Delgado as *Harpes* cf. *primus* (S.G. 1254) is a flattened internal mould of a nearly complete but poorly preserved exoskeleton. The cheek lobes appear to be smooth and there are nine to ten pits across the width of the brim anteriorly. The pits in the outermost arc are slightly smaller than the remaining fringe pits. There are an estimated twelve thoracic segments but the thorax/pygidium junction is difficult to interpret. The smooth cheek lobes and large number of pits across the anterior brim distinguished this species from other Armorican and Iberian species. The probable number of thoracic segments and lack of genal caecae in the Bougado species are features seen in *E. primus* but the Bohemian species has fewer pits across the brim. *E. benignensis* also has nine to ten pits across the anterior width of the brim but differs from the Bougado species in that it has a well-developed ornament on the cheek lobes. Until more material is available the Bougado specimen may not be confidently identified and is provisionally referred to *Eoharpes* sp. The other Bougado specimens identified by Delgado as *Harpes* sp. n. are two internal moulds of flattened, incomplete cranidia (S.G. 1256, 1258). The specimens are too poorly preserved to allow identification.

In the Valongo Formation, on the western limb of the Valongo Anticline (Romano and Diggens 1973–1974) east of Porto, *E. cristatus* occurs about 100 m above graptolites of the *D. murchisoni* Zone and, as in Brittany, it is associated with *P.* (*C.*) *tournemini.*

In central Portugal, Mação–Amendoa region, harpids are represented by *E. macaoensis.* The Ordovician stratigraphy of this region has received scant attention since the early work of Delgado who described the stratigraphy of the area and included extensive faunal lists (1908, pp. 80–84). In this region Delgado recognized Llanvirn graptolitic mudstones overlying basal Ordovician quartzites (text-fig. 2) containing the almost ubiquitous *Skolithos* and *Cruziana* ichnofacies. Succeeding the Llanvirn mudstones are the 'Schistes à *Homalonotus*', a sequence of sandstones in the lower part overlain by silty mudstones, which Delgado correlated with the 'Schistes à *Homalonotus Oehlerti*' of the Buçaco region. This latter unit was included in the Cacemes Formation by Mitchell (1974) who considered it to be of Lower Llandeilo age. More recently, however, Henry, Nion, Paris and Thadeu (1973–1974) and Paris (1979) have shown that the formation ranges up into the basal Caradoc. In the Amendoa–Mação region the 'Schistes à *Orthis Berthoisi*' succeed the 'Schistes à *Homalonotus*' and as well as yielding *E. macaoensis* also contain *Eccoptochile* (*Eccoptochile*) *clavigera* (Beyrich) (Romano 1980), *Selenopeltis buchi* (Barrande), *Primaspis?* sp. (Romano, in prep.), and *Actinopeltis.* Thus the assemblage is almost certainly of Caradoc age but since the overlying 'Quartzites et Schistes culminants' are virtually unfossiliferous (Delgado 1908) the upper age limit of the 'Schistes à *Orthis Berthoisi*' is not known.

The presence of *Eoharpes* and *Dionide* (Henry and Romano 1978) in Brittany and Portugal contrasts with the situation in Spain where, although otherwise similar faunas and sequences are known from the Luso–Alcudian Zone (Hammann and Henry 1978), as far as the authors are aware neither of these genera have been recorded. The reasons for this are not apparent but are presumably related to migration patterns and/or ecological constraints; although there does not appear to be any strong evidence for the latter.

CONCLUSIONS

The presence of *Eoharpes* from the Martigné-Ferchaud synclinorium in Brittany and in the Bougado and Valongo areas in north Portugal enforces the earlier suggestions of a close faunal resemblance between these areas during the Llandeilo (Henry *et al.* 1973–1974; Hammann and Henry 1978; Henry and Romano 1978) although with the eoharpids the resemblance is only at generic level. The probable younger age range of *E. macaoensis* suggests that in Portugal at least there was a possible southward migration of the group in terms of present-day geography during the Ordovician. This contrasts with an inferred northward migration for other trilobite genera such as *Dionide* and

Selenopeltis in Brittany and Iberia (Henry and Romano 1978; Bruton and Henry 1978) but it is interesting to note that in terms of the model proposed by Paris and Robardet (1977) the apparent migration directions of the trilobite groups in both Iberia and Armorica would be from 'east' to 'west'.

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SMALL TEMNOSPONDYL AMPHIBIANS FROM THE MIDDLE PENNSYLVANIAN OF ILLINOIS

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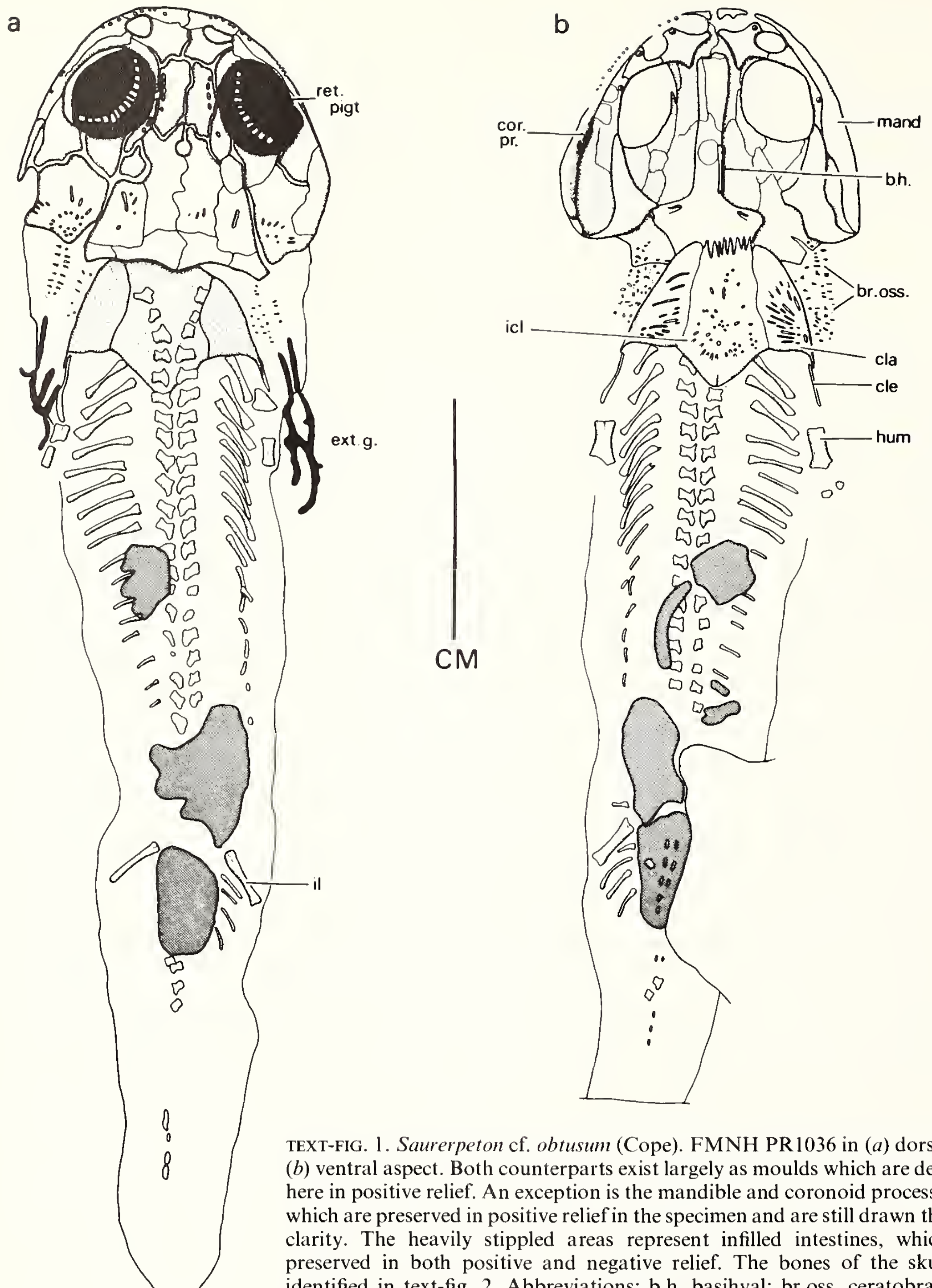
ABSTRACT. The small temnospondyl amphibians from the Middle Pennsylvanian Francis Creek Shale of Mazon Creek near Morris, Illinois, are redescribed together with recently collected Francis Creek Shale specimens from Pit 11 near Braidwood, Illinois. A well-preserved larval specimen of the trimerorhachoid *Saurerpeton* cf. *obtusum* represents a new record for the 'Mazon Creek' fauna. It demonstrates the presence of three pairs of external gills and rows of ceratobranchial dental ossicles modified as gill rakers in a larval saurerpetontid. *Amphibamus grandiceps* Cope from Mazon Creek and the contemporary *A. lyelli* (Wyman) from Linton, Ohio, are shown to be distinct species which can be diagnosed on several size-independent and size-linked characters. Three of the specimens of small larval temnospondyls from Mazon Creek are identified as the larvae of *A. grandiceps* whilst two others are referred to the genus *Branchiosaurus* and, as such, constitute another new record for the 'Mazon Creek' fauna. The shared similarities of *Amphibamus* and *Branchiosaurus* support a hypothesis that the branchiosaurids are a monophyletic or polyphyletic group of neotenous dissorophoids most closely related to the Dissorophidae.

The Francis Creek Shale fossil assemblages contain very few tetrapods, all of which appear to be transported erratics. They appear to have been mostly small terrestrial and pool-dwelling forms living on the levees of the delta-fan and having been inundated by a flood and washed into an offshore depositional area.

THE fossil assemblage from the Middle Pennsylvanian Francis Creek Shale of north-eastern Illinois includes a small number of well-preserved specimens of small tetrapods. The first to be described was *Amphibamus grandiceps* Cope 1865 collected from Mazon Creek. Subsequently about a score of tetrapod specimens in sideritic concretions were collected from the Mazon Creek locality and these were reviewed by Moodie (1916), Olson (1946), and Gregory (1948, 1950). With the advent of strip mining in the area, large volumes of concretion-bearing shale have been exposed and several new tetrapod specimens have been collected, principally from Pit 11 near Braidwood, Illinois. Of this new material, only some aïstopods (Turnbull and Turnbull 1955; Lund 1978) and a microsaur (Carroll and Gaskill 1978) have been described to date.

Most of the readily determinable specimens of temnospondyl amphibian in the Francis Creek Shale fauna have proved to belong to *A. grandiceps*, the specimens described as *Mazonerpeton longicaudatum* Moodie 1912 and *Miobatrachus romeri* Watson 1940 being referred to this taxon by Gregory (1950) and Bolt (1979). Several other specimens of very small, poorly ossified temnospondyls have been described as, or referred to *Micrerpeton caudatum* Moodie 1909 or *Eumicrerpeton parvum* Moodie 1911. Moodie (1916) considered these forms to be referable to the Branchiosauridae, a family of small neotenous temnospondyls, principally known from the Permo-Carboniferous of Europe. Gregory (1950) reassessed them and considered them to be possible *Amphibamus* larvae but strictly indeterminate. Boy (1974, p. 261) concluded that, while some of these specimens were *Amphibamus*-like, others resembled *Branchiosaurus sens. strict*. These larvae are redescribed here, together with a recently collected specimen from Pit 11, and further consideration is given to their systematic position. Several other specimens were described and named by Moodie, namely *Erierpeton branchialis*, *Erpetobrachium mazonensis*, *A. thoracatus* and *Mazonerpeton costatum*, all of which were considered to be indeterminate by Gregory (1950). I concur with this conclusion and these specimens are not considered further in this study. Finally, another recently collected temnospondyl specimen is described here for the first time and constitutes the first record of a trimerorhachoid from the Francis Creek Shale fauna.

[Palaeontology, Vol. 25, Part 3, 1982, pp. 635-664, pl. 64.]



TEXT-FIG. 1. *Saurerpeton* cf. *obtusum* (Cope). FMNH PR1036 in (*a*) dorsal and (*b*) ventral aspect. Both counterparts exist largely as moulds which are depicted here in positive relief. An exception is the mandible and coronoid process in (*b*) which are preserved in positive relief in the specimen and are still drawn thus for clarity. The heavily stippled areas represent infilled intestines, which are preserved in both positive and negative relief. The bones of the skull are identified in text-fig. 2. Abbreviations: b.h, basihyal; br.oss, ceratobranchial dental ossicles; cla, clavicle; cle, cleithrum; cor.pr, coronoid process; ext.g, external gills; hum, humerus; icl, interclavicle; il, ilium; mand, mandible; ret.pigt, retinal pigment.

Material described or referred to in this study belongs to the collections of the American Museum of Natural History (AMNH); the British Museum (Natural History) (BMNH); the Field Museum of Natural History, Chicago (FMNH); the Department of Geology, University of Newcastle upon Tyne (KC); the Museum für Naturkunde, Humboldt University, Berlin (MB); the Museum of Comparative Zoology, Harvard University (MCZ); the National Museum of Natural History, Washington (USNM), and the Peabody Museum, Yale University (YPM).

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA
Order TEMNOSPONDYLI
Superfamily TRIMERORHACHOIDEA
Family SAURERPETONTIDAE Chase 1965
Genus SAURERPETON Moodie 1909

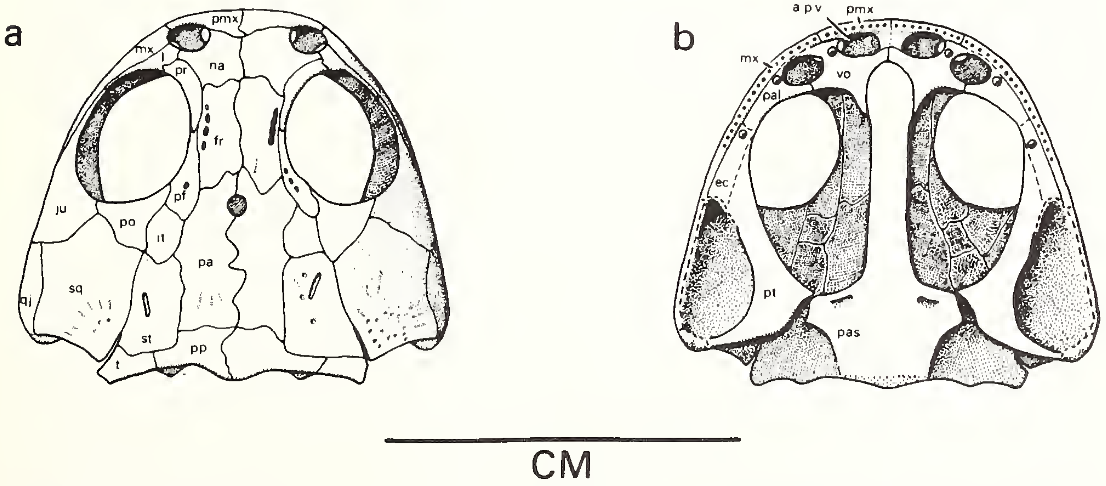
Type species. *Dendrerpeton obtusum* Cope 1868.

Saurerpeton cf. *obtusum*

Plate 64, figs. 1–4; text-figs. 1*a*, *b*, 2*a*, *b*
Material. FMNH PR1036 collected by Mr. J. Herdina of Berwyn, Illinois. At least two other specimens exist in private collections.

Locality. Peabody Coal Co. Pit 11 spoil heap, Will-Kankakee Counties, Illinois.

Horizon. Francis Creek Shale, Carbondale Formation, Desmoinesian, Middle Pennsylvanian (Westphalian D). The assemblage collected at Pit 11 is primarily of the marine Essex faunal type (Johnson and Richardson 1966) but contains some freshwater Braidwood faunal elements particularly at the northern end (Schram 1979, p. 176). The Braidwood faunal elements, including this specimen, are believed to have been washed into the sea by distributary flooding of the neighbouring swamps and delta levees (G. C. Baird 1979).



TEXT-FIG. 2. Reconstruction of skull of juvenile *Saurerpeton* cf. *obtusum* (Cope) based entirely on FMNH PR1036, (*a*) dorsal aspect, (*b*) palatal aspect. Abbreviations: a.p.v, anterior palatal vacuity; ec, ectopterygoid; fr, frontal; it, intertemporal; ju, jugal; l, lachrymal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pp, postparietal; pr, prefrontal; pt, pterygoid; qj, quadratojugal; sq, squamosal; st, supratemporal; t, tabular; vo, vomer.

DESCRIPTION

General features

The specimen is preserved in counterpart as a dorsoventral compression in the two halves of a sideritic concretion. Much of the kaolinite infilling has been removed, leaving moulds of both dorsal and ventral surfaces. Apart from the distal tail, the specimen is completely within the concretion although the fore limbs are very poorly preserved and the hind limbs are not visible. The specimen is small, the skull being 10 mm long and the snout to pelvis length being 33 mm. About 17 mm of tail is present.

Skull and mandibles

The general configuration of the skull is evident in text-figs. 1 and 2 and the following description is restricted to features of significance or interest. The construction of the skull closely resembles that of *Saurerpeton obtusum* from Linton, Ohio. Like the small, presumably juvenile specimens from that locality, it possesses proportionately large nares, orbits, pineal foramen and interpterygoid vacuities, simple sutures, very light pitting of the dermal bones, and traces of dermo-sensory pits on the frontals, postfrontals, and supratemporals. The reconstructions of the Linton *Saurerpeton* currently available in the literature are inadequate, being based on single incomplete specimens (Steen 1931, text-fig. 16; Watson 1956, text-fig. 24) or incompletely prepared material (Romer 1930, fig. 6; 1947, fig. 22). For this reason, a reconstruction of the skull of PR1036 has been prepared (text-fig. 2). Examination of casts of small *Saurerpeton* specimens from Linton has not revealed any significant features in which the Linton and Illinois specimens differ and the reconstruction may be taken to be representative of juvenile *Saurerpeton*.

The snout is abbreviated, the nasals are broader than long, and there is no internasal foramen. It is difficult to assess whether the large external nares represent a specific resemblance to the condition in *Acroplous* (Hotton 1959) or whether they are simply relatively large in a tiny individual. The asymmetry in the nasal region may be an artefact of compression although it does appear to be genuine and I have incorporated it in the reconstruction. The lachrymal extends from the external naris to the anterior orbit margin where it contacts the jugal. The jugal broadly borders the orbit margin. There is a prefrontal–postfrontal contact excluding the frontal from the orbit margin. Intertemporals are present. The posterior skull is elongate, particularly the parietals and supratemporals. The pineal foramen is situated at the anterior end of the interparietal suture. The postparietals have a stepped anterior edge, so that each one is the shape of a very thick L with the postero-distal end being as narrow as the tabular. The squamosals are squarish bones each with a shallowly concave posterior edge, presumably the vestige of an otic notch. This shape of squamosal is depicted in *Acroplous* by Hotton (1959) although he identifies a tiny gap between the squamosal and supratemporal as a rudimentary otic notch. I suspect that this is just the outer end of a very open suture, probably a line of kinesis between the cheek and the skull table occurring in all saurerpetontids. Boy (1974) cites D. Baird's observation that the Linton *Saurerpeton* apparently possesses lines of kinesis between the cheeks and the skull table. FMNH PR1036 (text-fig. 1*a*) shows the squamosal sharing a non-undulating common border with the supratemporal which may represent a line of kinesis extending forwards between the postorbital and the supratemporal. It seems to me to be more likely that the shallowly concave posterior edge of the squamosal should represent the margin of an otic structure, functional or rudimentary, than that the widened end of a kinetic line should have an otic homology.

As in most Francis Creek Shale vertebrates, each orbit contains a black disc which appears to be the retina preserved as a degraded pigment (Richardson and Johnson 1971, p. 1228). Also visible in each orbit is part of a sclerotic ring. The incomplete ring in the morphological right orbit (left in text-fig. 1*a*; Pl. 64, fig. 3) contains fourteen plates and suggests the presence of a typical temnospondyl sclerotic ring of about thirty plates. Examination of several specimens of *S. obtusum* from Linton, all of which are well preserved and in articulation, revealed one (MCZ 2487) which possessed an incomplete ring of ten plates in one orbit. The rarity of preserved sclerotic plates in otherwise well-preserved specimens is neither surprising nor significant, as these structures are encountered only rarely in other genera where they are known to occur. Examination by the author of over

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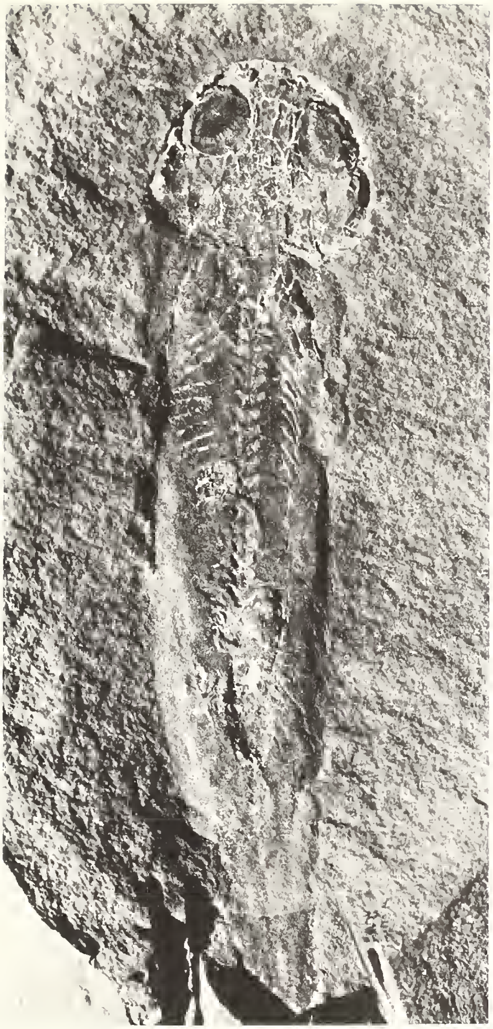
EXPLANATION OF PLATE 64

Figs. 1–2. *Saurerpeton* cf. *obtusum* (Cope), FMNH PR1036. Counterparts of concretion showing dorsal and ventral moulds of specimen, ×2·5.

Figs. 3–4. *Saurerpeton* cf. *obtusum* (Cope), FMNH PR1036. Dorsal and ventral moulds of the skull, ×3.



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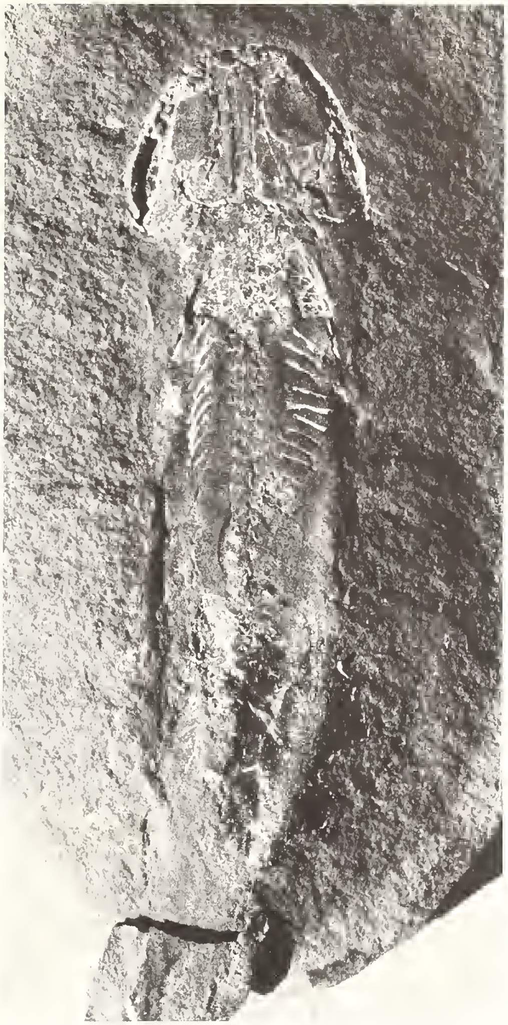

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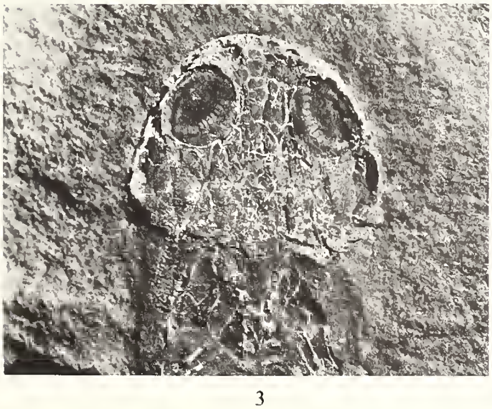

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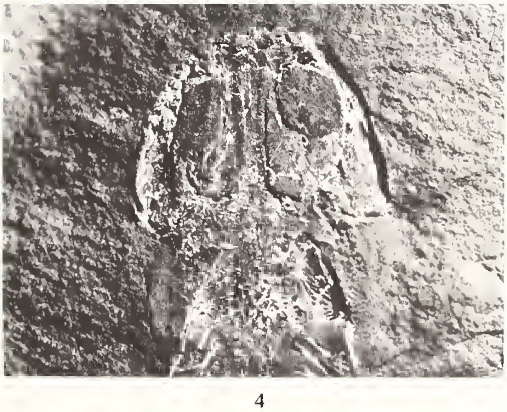


4

MILNER, temnospondyl amphibians

thirty skulls of *Cochleosaurus bohemicus* from Nýřany, Czechoslovakia, revealed only two specimens with sclerotic rings *in situ* although most of the material was preserved in articulation in a fine laminated coal. In both the Linton *Saurerpeton* and the Nýřany *Cochleosaurus* the widespread absence of sclerotic plates undoubtedly relates to prepreservational decomposition of the eyes of which the sclerotic plates are an integral part. The only trimerorhachoids in which sclerotic ossifications have been previously reported are the trimerorhachid *Lafonius* from the Upper Pennsylvanian of New Mexico (Berman 1973) and *Eugyrinus* from the Upper Carboniferous of England (Milner 1980*a*). No saurerpetontid has been previously reported with these structures.

The premaxilla and maxilla bear small marginal teeth, at least back to the level of the middle of the orbit. The small vomers bear a single pair of tusks anterior to the internal nares. The vomers form the mesial border of the internal nares and the posterior border of the paired anterior palatal vacuities. It is not possible to ascertain whether the vomers contact the palatines on the maxillary side of the internal nares as in *Acroplous*. The palatines are short V-shaped bones entering the margin of the interpterygoid vacuities and each bearing a single tusk. Ectopterygoid tusks are also visible although the bones themselves are not exposed. Each pterygoid has short palatine and quadrate rami and has a mobile contact with the braincase. The basal plate of the parasphenoid bears prominent carotid foramina and anterolateral 'wings' articulating with the pterygoids. The cultriform process is broad and appears to form a wedge between the vomers which have only a narrow sutural contact anterior to it. No denticles are visible on any palatal ossifications. The mandibles are poorly preserved and little can be made out except for the presence of a prominent coronoid process.

Hyobranchial skeleton

Superimposed on the cultriform process of the parasphenoid (text-fig. 1*b*) is a small rod-like ossification which is slightly expanded at both ends. Its shape and medial position indicate that it is a copula, a medial hyobranchial ossification of uncertain homology but probably the basihyal. Boy (1974) reported such an element in a large *Saurerpeton* from Linton (USNM 4471), an observation which I can confirm, although this ossification has not yet been described. Apart from the copula, the hyobranchial skeleton of FMNH PR1036 was not ossified but can be inferred as having been present from the presence of several rows of dental ossicles modified as gill rakers (text-fig. 1). These have not previously been reported in *Saurerpeton*. At least four rows of these tooth-bearing ossicles are visible in the branchial region on each side of the specimen and six rows were probably present on each side as in *Branchiosaurus* (Boy 1972, fig. 39). In well-preserved *Branchiosaurus* cf. *petrolei* specimens from Odernheim, the six rows can be seen to occur in a 1-2-2-1 configuration on each side of the branchial region (Bulman and Whittard 1926; Boy 1972). As Bulman and Whittard noted, this configuration is consistent with the dental ossicles on each side having been attached to four cartilaginous ceratobranchials bordering three gill-slits. The dental ossicles of larval temnospondyls appear to have functioned as gill rakers with spike-like denticles extending across each gill-slit from the ceratobranchials on either side of it and acting as a filter preventing small food particles from being lost via the gill-slits. In several living neotenous urodeles, non-respiratory gill-slits are bordered by non-skeletal papillae which serve this purpose (Noble 1931) and may even be the homologues of the dental ossicles (Stadtmüller 1936, p. 659). Richardson and Johnson (1971, p. 1230) reported that one unidentified small amphibian from the Francis Creek Shale has ostracods in its gut, and gill rakers would have been essential for feeding on such organisms.

Ceratobranchial dental ossicles or comparable ossicles have been reported in eight genera of Palaeozoic amphibian, seven of which are temnospondyls, the other being a microsaur. They are the trimerorhachid *Lafonius* (Berman 1973, text-fig. 5), the saurerpetontid *Saurerpeton* (this paper, text-fig. 1), the actinodontid *Sclerocephalus* (Boy 1972, figs. 11, 69), the archegosaurid *Archegosaurus* (Meyer 1857, pl. 14), the micromelerpetontids '*Limnerpeton*' (Milner, unpubl.) and *Micromelerpeton* (Boy 1972, fig. 11), the branchiosaurid *Branchiosaurus* (Boy 1972, fig. 11), and the microbrachomorph microsaur *Microbrachis* (Carroll and Gaskill 1978, figs. 77 and 78 as 'gill-supports').

The structure of individual dental ossicles has been well illustrated by Boy (1972) for *Branchiosaurus*, *Micromelerpeton*, and *Sclerocephalus* and Berman (1973) for *Lafonius*. The dental ossicles in FMNH PR1036 are not sufficiently well preserved for a consistent structure to be made out, but appear to have been rod-like ossicles with an expansion at one end, probably the insertion on the surface of the ceratobranchial. In this form, these structures must have functioned as gill rakers and would only have been of value to small aquatic plankton feeders. In forms such as *Sclerocephalus* and *Archegosaurus*, they occur only in the smallest individuals, presumably larvae, and are not retained in equally well-preserved adults. Their presence in a small *Saurerpeton* larva does not therefore imply that they were necessarily present in large individuals of the same species.

Ceratobranchial dental plates are a primitive character of the Osteichthyes (including Tetrapoda) and occur as platelets of bone bearing small teeth in such forms as the actinopterygian *Amia*, the osteolepiform *Eusthenopteron* (Jarvik 1980), and the coelacanth *Rhabdoderma* in which some of them also functioned as gill rakers (Forey 1981). Dental plates modified as branchial gill rakers were taxonomically widely distributed in temnospondyl larvae and may be taken as characterizing the primitive temnospondyl condition, having presumably been present in the larva of the common ancestor of the above-listed temnospondyls. The further presence of these ossicles in *Microbrachis* implies that the common ancestor of temnospondyls and microsaurs also possessed a larva with gill rakers. The relationships of the early tetrapods have yet to be established with any degree of certainty but the temnospondyls and microsaurs have never been suggested as being closely related to each other, implying that the presence of larval gill rakers is either a primitive tetrapod character or a retention of a similar condition from larval choanate fishes. Ceratobranchial dental ossicles seem to have been lost as an adult characteristic in tetrapods except for neotenous temnospondyls such as *Gerrothorax*, a late Triassic plagiosaur which appears to bear denticles on ossified ceratobranchials (Nilsson 1946).

Also present in FMNH PR1036 are the carbonized remains of the external gills. There appear to have been three filamentous external gills on each side as in *Branchiosaurus* and many living urodeles. There is not good evidence that the gill filaments were pinnate. External gills have not previously been reported in any trimerorhachoid although, as with the gill rakers, they may occur only in the larvae. The only temnospondyls in which external gills have been widely reported are *Branchiosaurus* from Odernheim (Bulman and Whittard 1926) and Friedrichroda (Whittard 1930) and *Tungussogyrinus* from the Permian Tunguska basin in Siberia (Efremov 1939). Also from Odernheim, the temnospondyls *Micromelerpeton credneri* (Malz 1967, figs. 7 and 8) and *Sclerocephalus* are occasionally preserved with small external gills visible. Thus larval eryopoids, dissorophoids, and trimerorhachoids all possessed external gills and in none of these forms can more than three pairs of gills be seeen, supporting Bystrow's (1939) contention that Palaeozoic amphibians possessed no more than three pairs of external gills. Sushkin (1936) and Schmalhausen (1968) have both argued that early tetrapods may have retained four pairs of external gills such as still occur in the larvae of lepidosirenid lungfish, recently argued to be the nearest living relatives of the tetrapods (Rosen, Forey, Gardiner and Patterson 1981). Sushkin's argument was based on the presence in the Upper Permian temnospondyl *Dvinosaurus* of a groove for a fourth branchial artery on the fourth ceratobranchial, implying the presence of a fourth external gill. Schmalhausen based his argument on the retention of a rudimentary fourth pair of external gills in the larva of the hynobiid salamander *Ranodon*, one of the most primitive living salamanders. The distribution of three or four pairs of external gills among Palaeozoic amphibians remains uncertain but in all small temnospondyls in which carbonized external gills can be counted, no more than three pairs are visible.

Postcranial skeleton

The vertebral column consists of an estimated twenty-four presacral vertebrae (two to three are obscured anterior to the pelvic region) and a few proximal caudal vertebrae are also preserved. Each vertebra consists of the paired halves of low neural arches but there are no ossifications corresponding to centra. The vertebrae thus correspond to the 'phyllospondyl' condition which is simply a poorly ossified labyrinthodont condition as pointed out by Romer (1939). The ribs are straight, slender and slightly expanded at both ends. The anterior ribs of the pectoral region are larger and more fully ossified than those further back. The tail was laterally flattened.

The pectoral girdle includes a large rhomboidal interclavicle, slightly longer than broad and with a pectinate anterior edge as found in several genera of Palaeozoic temnospondyls (*Eugyrinus*, *Acroplous*, and *Branchierpeton*). The clavicles are also proportionately large with broad triangular ventral blades overlapping the interclavicle. A tiny ossification representing the scapulo-coracoid is present as is a slender rod-like cleithrum. The fore limbs were tiny and only the shafts of the major limb bones are ossified. The humeri appear to have been short and stout. The ilium consists of a long slender blade expanded slightly at the acetabulum, resembling that of the Linton *Saurerpeton*. The ischia and pubes are not visible and may have been unossified. No hind limbs are visible. In the posterior abdominal region are several amorphous structures which, from their shape and position, appear to be endocasts of the intestines as reported by Moodie (1911) in some of the small temnospondyl larvae from Mazon Creek. No dermal scales are visible on the specimen.

SYSTEMATIC POSITION

PR1036 is clearly a small temnospondyl of the trimerorhachoid-brachyopoid complex, having an elongate skull-table, a poorly developed otic notch, paired anterior palatal fenestrae, a broad cultriform process, and reduced limbs. The retention of primitive tetrapod features such as the presence of intertemporals, a movable basipterygoid–basisphenoid articulation, and unossified ceratobranchials preclude it from being dvinosaur, kourerpetontid, or brachyopid, and identify it as one of the trimerorhachoids which characterize the late Palaeozoic tetrapod assemblages of North America. These Upper Carboniferous and Lower Permian forms are currently divided into two families, the Trimerorhachidae (including *Trimerorhachis*, *Neldasaurus*, and *Lafonius*) and the Saurerpetontidae (including *Saurerpeton*, *Acroplous*, and *Isodectes*). In recent years they have been the subject of studies by Hotton (1959), Chase (1965), Baird (1966—and in Welles and Estes 1969), Berman (1973), and, from a cladistic viewpoint, by Coldiron (1978). Chase's family group Saurerpetontidae is considered by Coldiron to be a paraphyletic grade and hence an artificial group in his hypothesis of relationships. The family name is retained in this work as a useful label for the *Saurerpeton-Acroplous-Isodectes* group. The Francis Creek Shale specimen may be identified as a saurerpetontid by the presence of the following characters as well as those listed above:

L-shaped postparietals and slender tabulars.
Jugal broadly entering the orbit margin.
Palatine broadly bordering the interpterygoid vacuity.
Absence of palatal denticles or tooth-rows.
Presence of a pronounced coronoid process on the mandible.
Presence of a kinetic line between the cheek and the skull-table.
A 'winged' basal plate to the parasphenoid.
Ilium with a long slender blade.

Referring the specimen to a given genus of saurerpetontid is rendered difficult by the unsatisfactory comparative diagnoses of the material available in the literature. *Saurerpeton* has not been studied recently and the older published first-hand descriptions are not entirely accurate. For example, acid-etching of the Linton material by Dr. D. Baird has revealed that it does not possess the distinct otic notches depicted by Romer (1947) and Watson (1956), the squamosals showing only shallow posterior concavities as in *Acroplous* and *Isodectes* (*Eobrachyops*). Furthermore, new specimens of *Acroplous* from the Lower Permian Speiser Shale of Kansas (Schultze 1980) and of *Isodectes* from the Upper Pennsylvanian Burlingame Limestone, also in Kansas (Baird 1966 and 1969 *in* Welles and Estes), have recently been collected and are currently being studied respectively by Mr. Brian Foreman and Mr. John Chorn of Kansas University, Lawrence, Kansas. Mr. Foreman and Mr. Chorn have kindly permitted me to examine their material and it is clear that a substantial re-evaluation of the characteristics of *Acroplous* and *Isodectes* will be necessary and that *Acroplous* at least possesses undescribed derived conditions not found in the Linton *Saurerpeton* or in the Francis Creek Shale specimen. The characters of the type of *Isodectes* from the Texas red-beds are ill-defined in the literature and this, combined with the close resemblance of the contemporary Linton and Francis Creek Shale specimens, leads me to refer the Francis Creek Shale specimen to the genus *Saurerpeton*.

The type species *Saurerpeton obtusum* is based on material described from the Westphalian D coal-swamp assemblage from Linton, Ohio. At least twelve specimens were collected at Linton and several were described under different names. The valid binomen is derived from *Dendrerpeton obtusum* Cope 1868 (AMNH 6928) and *S. latithorax* (Cope) Moodie 1909 (USNM 4471). Similar material has been described from the contemporary Kittanning Coal of Cannelton and is currently reported in the literature under the undiagnosed binomen of *S. minimum* (Moodie 1909), see D. Baird 1964, 1978. It is probably not distinguishable from *S. obtusum*. The Francis Creek Shale is contemporaneous with the Linton and Cannelton horizons and the *Saurerpeton* specimens from all three localities are extremely similar. As the two named species have not been comparatively diagnosed and are doubtfully distinct, the Francis Creek Shale specimen is referred to *S. obtusum* as the senior species. Ultimately, comparative study of the material from the three localities may reveal from one to three species.

Superfamily DISSOROPHOIDEA
Family DISSOROPHIDAE Williston 1910
Genus AMPHIBAMUS Cope 1865

Type species. *Amphibamus grandiceps* Cope 1865.

Diagnosis. Primitive dissorophids growing to about 300 mm total length. The skull is unusually broad in large specimens, being almost circular in dorsal aspect, and the skull table is more abbreviated than in any other dissorophoid with the occiput being clearly anterior to the level of the quadrates. Other characteristics of the genus are primitive retentions as *Amphibamus* lacks several of the derived conditions characterizing most or all other dissorophids. Retained primitive features include the presence of a prefrontal–postfrontal suture, the presence of a stapedial foramen, the absence of dermal armour plates on the tops of the neural spines, and the absence of rugose ridges on the dermal skull roof. All described material is from the Westphalian D of North America and Europe.

Amphibamus grandiceps Cope 1865

Text-figure 3*a*, *b*

Diagnosis. (For 'post-metamorphic' material only.)

As for genus, plus:

Parasphenoid bears a slender cultriform process with a single medial row of denticles.

Space for forty-eight marginal teeth in each jaw ramus.

Twenty to twenty-one presacral vertebrae.

Ossified ventral dermal scales present.

At 14 mm mid-line skull length, the skull of *A. grandiceps* has the following characteristics: undulating medial sutures between frontals and parietals; postfrontals expanded posteriorly behind level of posterior orbit margin; and pineal foramen posterior to level of posterior orbit margin.

(See remarks below for discussion of this diagnosis.)

Selected synonymy. (For 'post-metamorphic' material only.)

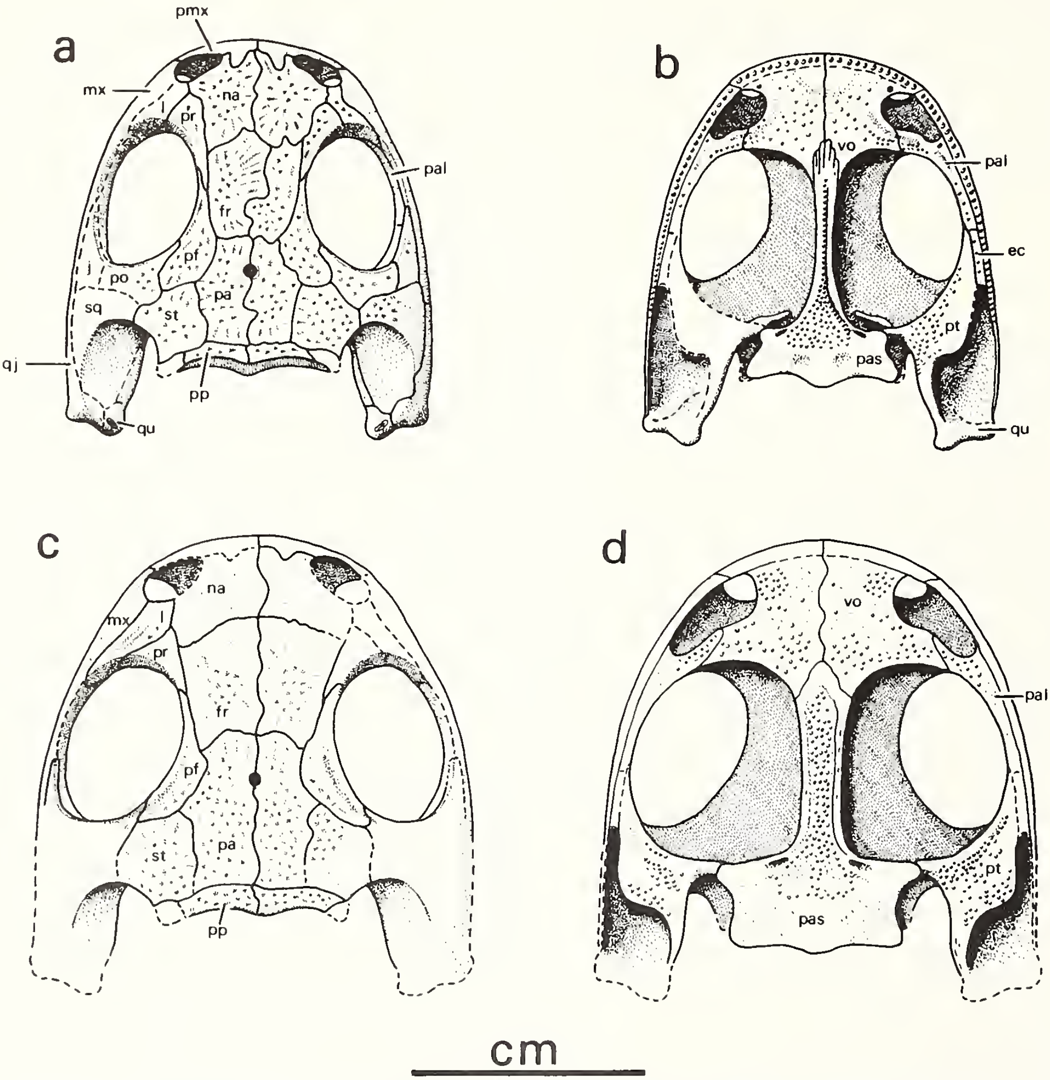
1865 *Amphibamus grandiceps* Cope, p. 134.
1866 *Amphibamus grandiceps* Cope; Cope, p. 135, pl. 32, fig. 8.
1912 *Mazonerpeton longicaudatum* Moodie, p. 337, pl. 3, figs. 1, 2; pl. 7, fig. 3.
1916 *Mazonerpeton longicaudatum* Moodie; Moodie, p. 61, pl. 3, figs. 5, 6; text-fig. 14*a*.
1916 *Amphibamus grandiceps* Cope; Moodie, p. 126, pl. 3, fig. 7; pl. 4, figs. 5, 6; pl. 14, figs. 1, 2; text-figs. 26–28.
1940 *Amphibamus grandiceps* Cope; Watson, p. 195, fig. 1.
1940 *Miobatrachus romeri* Watson, p. 198, figs. 2–10.
1950 *Amphibamus grandiceps* Cope; Gregory, p. 841, figs. 1–6.
1964 *Amphibamus grandiceps* Cope; Carroll, p. 242.
1979 *Amphibamus grandiceps* Cope; Bolt, p. 529, figs. 1–3, 5–9.

Surviving material. YPM 794, the neotype of *A. grandiceps*. YPM 795, the type of '*Mazonerpeton longicaudatum*'. FMNH UC2000, the type of '*Miobatrachus romeri*'. FMNH PR558, an undescribed but poorly preserved specimen in counterpart.

The holotype of *A. grandiceps* was destroyed in a fire (Moodie 1916, p. 126) and a further specimen (Moodie 1916, pl. 14, figs. 1, 2) is now unlocatable (Gregory 1950, p. 842).

Localities and horizons. The five described specimens all appear to have been collected in Mazon Creek, near Morris, Grundy County, Illinois. The undescribed FMNH PR558 is from the Pit 11 spoil heap, Will-Kankakee Counties, Illinois. All are from the Francis Creek Shale, Carbondale Formation, Desmoinesian, Middle Pennsylvanian (= Westphalian D).

Remarks. The above synonymy and list of material is incorporated for the sake of completeness. The material has been studied in recent years by Gregory (1950), Carroll (1964), and Bolt (1979) and Dr. J. R. Bolt is undertaking further study of it. The reconstruction of the skull (text-fig. 3*a*, *b*) is primarily based on YPM 794 although the jaw suspensorium incorporates information from FMNH UC2000. It is an original reconstruction based on first-hand examination of latex casts, but does not include any new information which cannot be gleaned from the recent published work listed above.



TEXT-FIG. 3. Reconstructed skulls of small post-metamorphic individuals of *Amphibamus*. (*a*, *b*) *Amphibamus grandiceps* Cope from Mazon Creek. Reconstruction of skull roof and palate based on YPM 794 with details of the jaw suspensorium and otic region based on FMNH UR2000. (*c*, *d*) *A. lyelli* (Wyman) from Linton, Ohio. Provisional reconstructions of the skull roof and palate based on MB 1888-1456. Abbreviations: ec, ectopterygoid; fr, frontal; j, jugal; l, lachrymal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pp, postparietal; pr, prefrontal; pt, pterygoid; qj, quadratojugal; qu, quadrate; sq, squamosal; st, supratemporal; vo, vomer.

The reconstruction is provided in order to facilitate comparison with a reconstruction of a similar size skull of *Amphibamus lyelli* in order to establish some diagnostic characters of the two species.

The species of Amphibamus

Carroll (1964) demonstrated that '*Pelion*' *lyelli* from the Westphalian D of Linton, Ohio, was, when stripped of some *Saurerpeton* specimens, sufficiently similar to *A. grandiceps* as to merit inclusion in the same genus, as the new combination *A. lyelli.* Bolt (1979, p. 552) concurs with this. Carroll also referred contemporary material from Nýřany, Czechoslovakia, to the genus as the new combination *A. calliprepes* (Steen). This material requires redescription before it can be comparatively diagnosed against the North American species of *Amphibamus* and it is not discussed further here except to note that, from my examination of the material, it is indeed a distinct species, either of *Amphibamus* or a closely related but distinct genus.

Carroll (1964) differentiated the two North American species of *Amphibamus* on the following criteria which appeared to him to be size-independent.

(i) Marginal tooth-rows. The number of tooth-spaces per jaw ramus is forty-eight in *A. grandiceps* and seventy-six in *A. lyelli.*
(ii) Number of presacral vertebrae. *Circa* twenty-one in *A. grandiceps* and twenty-five in *A. lyelli.*
(iii) Prefrontal–postfrontal suture. Relatively wide in *A. grandiceps* and relatively narrow in *A. lyelli.*
(iv) Postparietals. Relatively anteroposteriorly deep in *A. grandiceps* and relatively slender in *A. lyelli.*

However, the largest surviving specimen of *A. grandiceps* has a mid-line skull length of 14 mm whilst the smallest *A. lyelli* available to Carroll had a mid-line skull length of 26 mm, the other *A. lyelli* skulls being up to 50 mm long. Thus the possibility exists that some or all of these characters might actually be the product of ontogenetic changes rather than species-diagnostic characters and Bolt (1979, p. 552) has suggested that further study might result in the conclusion that the two populations were, to all intents and purposes, conspecific. Bolt also notes other differences in the marginal dentition (pedicellate teeth in *A. grandiceps*, conical teeth in *A. lyelli*) and presacral vertebral construction (gastrocentrous in *A. grandiceps*, rhachitomous in *A. lyelli*) which he suggests may also represent ontogenetically changing features in a single growth series.

I have been able to resolve some of these character differences as being ontogenetic or specifically diagnostic by reference to a hitherto undescribed small specimen of *A. lyelli* from Linton. A latex cast of this specimen MB 1888-1456 has been made available to me through the generosity of Dr. R. L. Carroll and Dr. R. Reisz. It is preserved in counterpart and is the anterior half of a small *A. lyelli* with a 17 mm long skull. It is thus only slightly larger than the neotype of *A. grandiceps* (14 mm skull) and permits the identification of character differences which are non-ontogenetic or the product of different rates of ontogeny. I hope to describe MB 1888-1456 more fully at a later date but include here a provisional reconstruction of the skull to facilitate comparison (text-fig. 3*c*, *d*).

It can be seen from text-fig. 3*a*–*d* that the 14–17 mm skulls of the two species are broadly comparable in the possession of proportionately large orbits, nares and pineal foramen that characterize juvenile temnospondyls. Both also lack any trace of lateral-line pits or sulci. Characters (iii) and (iv) used by Carroll (1964) to differentiate the two species appear to be simply the products of ontogeny. Comparison of text-figs. 3*a* and 3*c* shows the prefrontal–postfrontal sutures to be very similar in width and the postparietals to be equally slender in both skulls. The character-states for (iii) and (iv) which Carroll ascribes to *A. lyelli* are those of a larger *Amphibamus* skull and not necessarily species-diagnostic. Likewise MB 1888-1456 does not possess vomerine or palatine tusk-pairs (the ectopterygoids are obscured by the mandibles) although larger *A. lyelli* skulls do possess such tusks (Carroll 1964). This then is also an ontogenetic feature. Another feature of all small *Amphibamus* skulls of both species is the absence of tabulars. MB 1888-1456 has both tabulars missing as do all *A. grandiceps* specimens. Tabulars are certainly present in larger *A. lyelli* specimens (AMNH 6841, BMNH R2670) indicating that their absence in smaller skulls is due to post-mortem detachment rather than natural absence or non-ossification. It is unlikely that the tabulars are only apparently absent due to delayed ossification as Boy's studies on ossification sequences in temnospondyls show the tabulars to ossify in the middle larval phase prior to the circum-orbital series (Boy 1974, table 1).

However, in some ontogenetically variable features, the two *Amphibamus* skulls do differ as follows:

(*a*) The 14 mm long *A. grandiceps* skull shows some interdigitation of the medial sutures between the frontals and parietals (a feature associated with older individuals) while the 17 mm long *A. lyelli* skull has simpler sutures.

(*b*) The *A. grandiceps* skull has a parietal foramen which is situated more posteriorly relative to the orbits than in the *A. lyelli* skull, suggesting again a greater ontogenetic age for the *A. grandiceps* skull.

(*c*) The postfrontals are posteriorly expanded in the *A. grandiceps* skull but are slender crescent-shaped bones in the *A. lyelli* skull. In larger *A. lyelli* (BMNH R2670) the postfrontals are also expanded posteriorly, indicating that this expansion takes place ontogenetically in *A. lyelli* but has not yet occurred in MB 1888-1456 although it has already occurred in the smaller *A. grandiceps* YPM 794.

Thus three separate cranial features suggest that *A. grandiceps* at 14 mm skull length is ontogenetically older than *A. lyelli* at 17 mm skull length. *A. lyelli* is known to grow to 60 mm mid-line skull length whereas *A. grandiceps* is not known to have grown to more than 20 mm skull length. This may be more than negative evidence. If *A. grandiceps* matured at a smaller size than *A. lyelli*, it is probably because it had a smaller adult size. Whether this was so or not, the difference in relationship of size and ontogenetic development in the two species is a diagnostic character.

Four apparently size-independent characters further serve to distinguish *A. grandiceps* from *A. lyelli*, two of which were reported by Carroll and two of which are recorded here for the first time.

(*d*) As noted by Carroll (1964), the number of marginal teeth in *A. grandiceps* is forty-eight per ramus whereas in *A. lyelli* it is about seventy-six per ramus. MB 1888-1456 does not possess a visible complete tooth-row but one sequence of twenty-two teeth and spaces is visible at the back of the right maxilla and these suggest a total per ramus of sixty to seventy although this sequence may include smaller posterior teeth. However, the discrepancy of tooth-counts between species seems too great to be a by-product of ontogeny because, although the number of teeth is known to increase with growth in some temnospondyls, this is much less dramatic. In Bystrow and Efremov's (1940) description of *Benthosuchus sushkini*, they report a 28 mm long skull with fifty-three premaxillary + maxillary teeth (op. cit., fig. 58) and a longer snouted 124 mm skull with seventy-four marginal teeth (op. cit., fig. 30). The proportional length of the snout increases with growth in *Benthosuchus* and the increase in numbers of marginal teeth is a consequence of this and the greater discrepancy in size between the two *Benthosuchus* specimens. In the two *Amphibamus* species, the difference in marginal tooth-count is greater considering that no snout elongation occurs, and is probably a valid specific difference.

(*e*) The other distinction recorded by Carroll (1964) which seems indisputable is the number of presacral vertebrae. In the type of *A. lyelli* (AMNH 6841) there are certainly twenty-five presacrals while in *A. grandiceps* there are either twenty or twenty-one (Bolt 1979, p. 547).

(*f*) As can be seen in text-fig. 3, the two species differ in the width of the medial region of the skull, *A. lyelli* having broader medial-region ossifications than *A. grandiceps*. On the dorsal surface of the skull, this is most conspicuous for the nasals and frontals, whilst in the palate, the parasphenoid shows the difference in width most obviously. In both *A. grandiceps* specimens with good parasphenoids (YPM 794 and UC2000), the cultriform process bears a single medial row of denticles along most of its length and the basal plate is antero-posteriorly narrow. In *A. lyelli* (MB 1888-1456) the cultriform process bears a broad medial strip of denticles, about four denticles in width and the basal plate is much less narrow antero-posteriorly.

(*g*) Dr. Donald Baird (*in litt.*) has pointed out to me, and I have subsequently confirmed for myself, that whereas the *A. grandiceps* specimens all possess chevrons of ossified gastralia (ventral dermal scales), no *A. lyelli* specimens show any trace of ossified scales. The preservation of vertebrates from Linton is extremely fine and all the *Amphibamus* specimens are articulated and show no evidence of disintegration, dermal structures such as the palpebral cup being present. As most other Linton tetrapods have prominent dermal scales present, one must conclude that *A. lyelli* lacked ossified scales throughout its known size range whereas *A. grandiceps* retained them. The absence of scales in *A. lyelli* inevitably suggests that it may have been one of the earliest amphibians to adopt cutaneous gas-exchange through a vascular skin.

Thus the two North American species of *Amphibamus*, though similar, can be distinguished by seven characters (*a–g* above), some of which reflect different rates of ontogenetic change (*a–c*) while others are more or less size-independent (*d–g*). Other differences between the two species, which Bolt (1979) has attributed to ontogenetic processes may yet prove to be divergent adaptations. The pedicellate teeth and pleurocentrum-dominated presacral vertebrae of *A. grandiceps* may or may not metamorphose into the conical teeth and rhachitomous vertebrae of the larger *A. lyelli*. Unfortunately MB 1888-1456 sheds no light on these characters. The possibility remains, however, that *A. grandiceps*, *Doleserpeton annectens*, and some of the small *Tersomius* material may represent a radiation of small unarmoured dissorophids uniquely characterized by pedicellate teeth and gastrocentrous vertebrae while the other larger, mostly armoured, dissorophids retained rhachitomous vertebrae and simple teeth throughout their life-history.

THE MAZON CREEK 'BRANCHIOSAURS'

Between 1909 and 1916 Moodie described a series of very small temnospondyl specimens from Mazon Creek under a variety of names as outlined in the introduction. He noted their resemblance to the European *Branchiosaurus* material and referred them to the Branchiosauridae. Romer (1939) demonstrated that the characteristics of the amphibian order Phyllospondyli (the 'branchiosaurs') were those of small or larval labyrinthodonts and concluded that most 'branchiosaurs' were the larvae of contemporary larger temnospondyls. Gregory (1950) comprehensively reviewed the Mazon Creek 'branchiosaurs', concluding that several of Moodie's specimens were completely indeterminate and that the remaining material represented a single type of temnospondyl larva. The senior name for this material was *Micrerpeton caudatum* and Gregory concluded that it was strictly indeterminate although possibly the larvae of *A. grandiceps*. Gregory's reluctance to place this material in the synonymy of *A. grandiceps* was based, in part, on five observable different characters (1950, p. 862) quoted here:

1. Skull length $\frac{1}{8}$ to $\frac{1}{5}$ total length, compared to about $\frac{1}{4}$ total length in *Amphibamus*.
2. Skull width appreciably greater than skull length instead of about the same.
3. Tail longer.
4. Pineal foramen between orbits instead of behind them.
5. Possibly less-developed horn on tabular (or supratemporal).

However, Gregory noted that all these characters were susceptible to alternative explanations (ontogenetic change, artefacts of preservation), but also argued that *M. caudatum* showed no positive resemblances to *A. grandiceps* and could have been the larval form of almost any contemporary temnospondyl. Boy (1971, 1972) has subsequently demonstrated the distinct nature of the Branchiosauridae as a family of small neotenous dissorophoids and has commented (1974) that some of the Mazon Creek larvae resemble *Amphibamus*, taking ontogenetic changes into account, while others bear a closer resemblance to *Branchiosaurus sensu stricto*. My re-examination of all the material, including the previously undescribed specimen FMNH PR664 from Pit 11 (text-fig. 4), has led me to agree with Boy's conclusion. The following systematic re-assessment of the Francis Creek Shale larvae (i.e. from both Mazon Creek and Pit 11) is restricted to five potentially determinable specimens—namely FMNH UR38 (the type of *M. caudatum*), FMNH PR664, USNM 4400, YPM 802, and YPM 803 (the type of *Eumicrerpeton parvum*). I agree with Gregory's conclusion that the type and only specimens of *Erierpeton branchialis* (YPM 801), *Mazonerpeton costatum* (YPM 800), *Erpetobrachium mazonensis* (YPM 799), and *A. thoracatus* (USNM 4306) are all indeterminate.

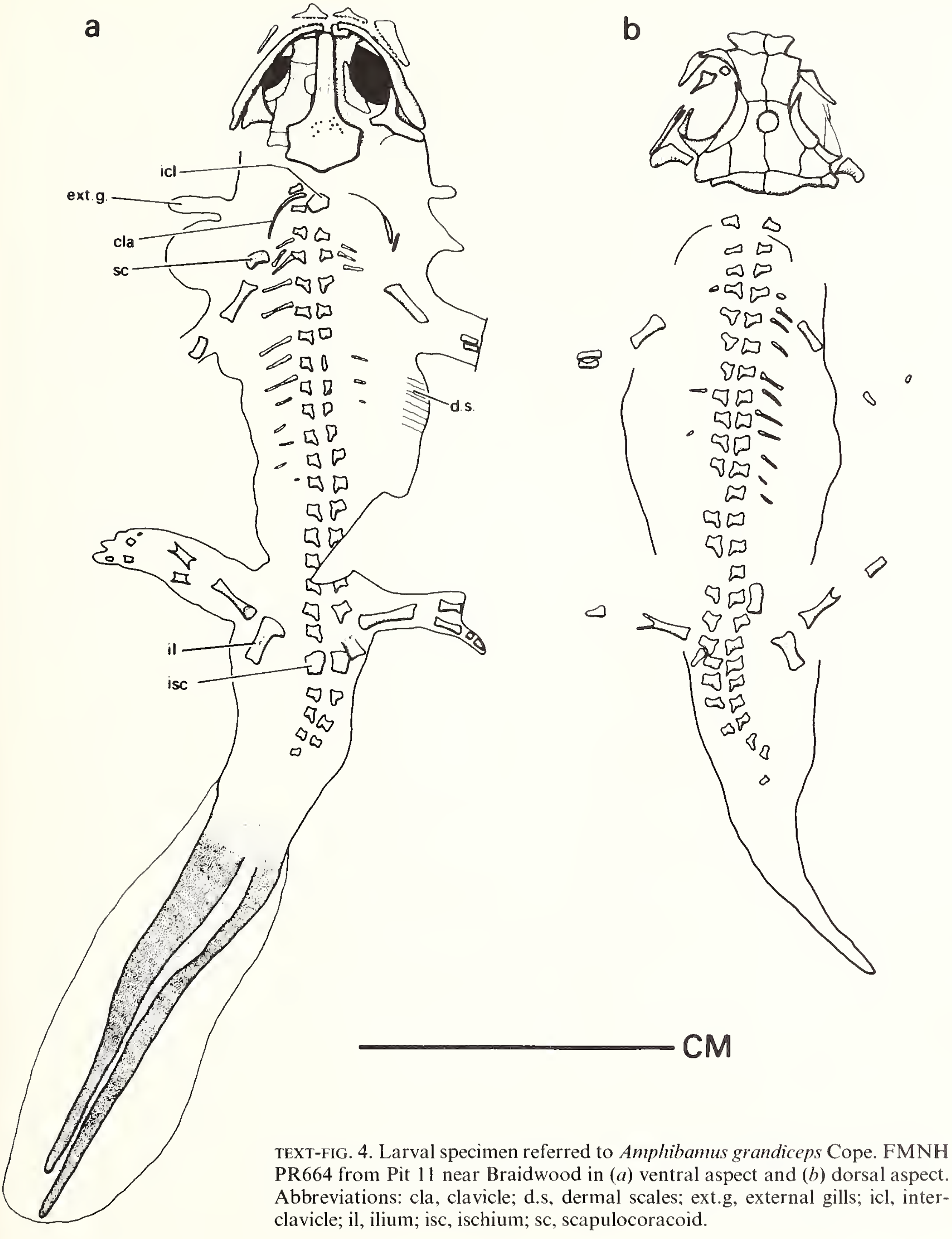
The five specimens studied are all certainly small temnospondyls and have the potential to be:

(i) Larvae of *A. grandiceps* which occurs in the same assemblage.
(ii) Small specimens of *B. sensu stricto* to which they bear a general resemblance and which occurs in the contemporary assemblage from Nýřany, Czechoslovakia. The earliest record of *Branchiosaurus* in North America is the only specimen of *B. darrahi* from the slightly younger Stephanian horizon at Montrose, near Pittsburgh, Pennsylvania.
(iii) Larvae of some other temnospondyl, known or unknown.

The characters that Gregory used to differentiate the Mazon Creek larvae from *Amphibamus* are mostly, as he himself observed, known to change during ontogeny or be susceptible to other explanations. The apparently relatively greater skull length of *Amphibamus* (Gregory, characters 1 and 2) is partly attributable to a slight increase in relative skull length produced by the posterior movement of the dissorophid jaw suspensorium during ontogeny to give a deeper gape for terrestrial feeding while retaining a large otic notch. The skull: total length ratio is also in part an artefact (as is Gregory character 3) of the lack of a complete tail in any specimen of *A. grandiceps* which, as Gregory notes, effectively negates the characters of tail length and ratio of skull length to total length. If, as seems possible from the work of Watson (1940) and Bolt (1979), *Amphibamus* is the closest Carboniferous relative of the Anura, then the reduction of the size of the tail at metamorphosis is more to be expected in *Amphibamus* than in any other Carboniferous temnospondyl. The width to length ratio of the skull (character 2) is partly attributable to the different degree of post-mortem crushing in the large and small skulls. In the small skulls, the cheeks and mandibles are spread out to the side to a much greater extent than in the larger *Amphibamus* skulls. The pineal foramen position relative to the orbits (Gregory, character 4) most certainly does shift backwards during ontogeny within a temnospondyl species as demonstrated by Bystrow and Efremov (1940) in *Benthosuchus sushkini.* The 'tabular' shape (character 5) is, in fact, the supratemporal shape, the tabulars being detached in USNM 4400 but visible as tiny ossifications in FMNH UR38 and PR664. The tabulars, and possibly the underlying distal edge of the supratemporal, elongate anteroposteriorly with growth, providing support for the dorsal edge of the tympanum in those forms which have a large otic notch such as *Dendrerpeton* (Milner 1980*a*) and *A. lyelli* (Steen 1931, text-fig. 11). Thus Gregory's characters do not preclude the Mazon Creek larvae from being synonymous with *A. grandiceps* and can all be attributed to ontogenetic changes or to artefacts of preservation. Gregory noted that this was not enough to justify assigning them to *A. grandiceps* as many of the features of the larvae were equally consistent with their being juveniles of other temnospondyls and they showed no special resemblance to *A. grandiceps*. This observation was substantially influenced by Romer's (1939) view that 'branchiosaurs' all metamorphosed into larger temnospondyls and hence that all their characteristics were merely those of larvae. As Boy (1972) has demonstrated, *Branchiosaurus sensu stricto* is not a larval taxon and many of the characters of this genus have systematic validity.

In order to attempt the determination of the 'Mazon Creek larvae', ten of their observable characters were identified and the distribution of these characters, both primitive and derived, among other Palaeozoic temnospondyls, was examined. The ten characters together with their status and general distribution are as follows, the sequence of characters commencing with the widespread primitive features and leading to the more precisely defining derived characters.

1. Preorbital region is very abbreviated. Probably both a primitive and larval tetrapod character retained in branchiosaurids, dissorophids, most trimerorhachoids, *Dendrerpeton*, and small larvae of long-snouted temnospondyls.
2. Prefrontal–postfrontal contact. A primitive tetrapod character, widespread in early temnospondyls but most dissorophids and branchiosaurids share a derived condition in which the reduced prefrontal and postfrontal do not meet and the frontal enters the orbit margin. However, *Amphibamus* and some primitive species of *Branchiosaurus* retain the primitive condition.



TEXT-FIG. 4. Larval specimen referred to *Amphibamus grandiceps* Cope. FMNH PR664 from Pit 11 near Braidwood in (*a*) ventral aspect and (*b*) dorsal aspect. Abbreviations: cla, clavicle; d.s, dermal scales; ext.g, external gills; icl, interclavicle; il, ilium; isc, ischium; sc, scapulocoracoid.

3. Large interpterygoid vacuities, palatine rami of the pterygoids with concave mesial margins. A derived character within the temnospondyls, occurring in most temnospondyls, the Anura, the microsaur *Hyloplesion*, and the diplocauline nectrideans. Primitive temnospondyls such as the colosteids, loxommatoids, *Edops*, and *Caerorhachis* all possess small or no interpterygoid vacuities as do the ichthyostegids and choanate fish.
4. Intertemporals absent. A derived condition within the temnospondyls although widespread in post-Carboniferous forms. Intertemporals are retained in most Carboniferous temnospondyls, only the loxommatid *Megalocephalus*, the colosteids *Colosteus* and *Erpetosaurus*, and the dissorophoids and eryopids lacking them.
5. Large otic notch extending as a shallow or deep concavity from tabular to quadrate and hence a relatively large structure occupying the entire posterior edge of the squamosal. This appears to be a derived condition characterizing *Dendrerpeton* and the Dissorophoidea (comprising the Dissorophidae, Trematopidae, Micromelerpetontidae, and Branchiosauridae). The primitive tetrapod and temnospondyl condition is either no notch or a small spiracular-type otic notch bordered by the tabular, supratemporal and part of the squamosal but not extending to the quadrate. The former condition occurs in colosteids, nectrideans, microsaurs, and captorhinomorphs, the latter condition occurs in ichthyostegids, loxommatids long-snouted edopoids, and eryopoids. In *Dendrerpeton* and the dissorophoids, the enlargement of the notch and, by implication, the tympanum, to occupy most of the posterolateral region of the head, is a derived condition not occurring in other early tetrapods, except by obvious convergence in some seymouriamorphs.
6. Jugal terminating in a point anteriorly and failing to contact the lachrymal. The primitive tetrapod and temnospondyl condition is a broad sutural contact between lachrymal and jugal at the level of the anterior orbit margin. In the Dissorophoidea and many of the Trimerorhachoidea, the larger orbits are distally bordered by the maxillae and the lachrymal and jugal do not meet. In larger individuals with proportionately small orbits, the cheeks tend to be broader or deeper but instead of reversion to the primitive condition, the intervening 'gap' is filled by the palatine (Dissorophoidea and Saurerpetontidae, see Bolt 1974*b*) or the postorbital (Trimerorhachidae).
7. Relatively long slender humerus, lacking a supinator process. The primitive tetrapod humerus as found in ichthyostegids, anthracosaurs, and colosteids is a stout 'tetrahedral' structure and in most temnospondyls it is a short 'waisted' bone with expanded ends and a prominent supinator process. However, in dissorophids (DeMar 1968) and branchiosaurids (Boy 1972), the humerus is more than twice as long as its greatest width and lacks a supinator process. Other dissorophoids such as the trematopids retain a short humerus with supinator process (DeMar 1968).
8. Slender clavicles and a relatively small interclavicle which is wider than long and has no posteromedial stem. Within the temnospondyls, this is a derived condition restricted to *Branchiosaurus*, some dissorophids (including *Amphibamus*), and also *Eryops*. The majority of temnospondyls, including primitive forms such as *Greererpeton*, *Dendrerpeton*, *Cochleosaurus*, and the trimerorhachoids, possess large, rhomboidal, heavily ornamented interclavicles bordered by clavicles with large broadly triangular blades. In the derived state, the clavicle blades are narrow and the interclavicle is a small bone, poorly ossified or unossified in *Branchiosaurus* but always slightly wider than long.
9. Twenty to twenty-two vertebrae. Most temnospondyls have twenty-five or more presacral vertebrae and there is no evidence to suggest that the primitive tetrapod or primitive temnospondyl condition were characterized by less than twenty-five presacrals. A smaller number occurs in *Eryops* (twenty-three) and in several, but not all, dissorophoids including *Cacops aspidephorus*, *Amphibamus grandiceps*, and *Branchiosaurus* spp. (twenty to twenty-one) and appears to represent a derived condition in these forms.
10. Extremely abbreviated skull-table, the tabular-tabular width being almost twice the length from the posterior orbit margin to the tabular. Among the temnospondyls, this type of

abbreviated skull-table appears to occur in a few eryopoid (*Eryops*, *Zatrachys*) and dissorophoid (*Branchiosaurus*, *Amphibamus*, *Broiliellus*) genera, and thus appears to be a derived character of at least double origin. The skull-table is relatively conservative in shape during ontogenetic change and the larvae of most temnospondyls do not have such abbreviated skull-tables as *Amphibamus* or *Branchiosaurus* (e.g. *Saurerpeton* larva—this paper, *Micromelerpeton* and *Sclerocephalus* larvae—Boy 1972, fig. 69).

Of the above listed ten characters, FMNH PR664 shares 1–10; USNM 4400 shares 1–5 and 7–10; FMNH UR38 shares 1–4, 7, 9, and 10; YPM 803 shares 1–3, 5, 8, and 10; and YPM 802 shares 1, 3, 8, and 10. The only described temnospondyl genera which include species sharing all ten characters, particularly derived characters 7–10 combined with primitive character 2, are the primitive dissorophoids *Amphibamus* and *Branchiosaurus*. None of the Francis Creek Shale larvae have characters inconsistent with their being either *A. grandiceps* larvae or small *Branchiosaurus* and there is no reason to conclude that they are anything other than one of these two. My initial attempts to identify all of these larvae as belonging to one of these two genera failed with the realization that some shared further characters with *Amphibamus* while others of similar size shared characters with *Branchiosaurus*. I have finally concluded that three of the specimens are larvae of *Amphibamus* while the other two are probably specimens of *Branchiosaurus*. They are discussed separately in the following systematic section together with the reason for the generic assignments.

Family DISSOROPHIDAE Williston 1910
Genus AMPHIBAMUS Cope 1865
Amphibamus grandiceps Cope (attributed larvae)

Text-figs. 4, 5*a–d*, *f*, *g*, 6*b*

Selected synonymy. (Larvae only.)

1909 *Micrerpeton caudatum* Moodie, p. 39, figs. 1–6.
1916 *Micrerpeton caudatum* Moodie; Moodie, p. 52, pl. 2; pl. 52, fig. 4.
1916 *Eumicrerpeton parvum* Moodie; Moodie, p. 57 *partim*! *non* Moodie 1910, 1911.
1950 *Micrerpeton caudatum* Moodie; Gregory, p. 857, figs. 7, 9 *partim*!

Included material. FMNH UR38 (previously Walker Museum 12313) (text-fig. 5*c*, *d*). The type (in counterpart) of *M. caudatum* figured extensively by Moodie. Gregory's figure (1950, fig. 7) is difficult to relate to the original specimen. USNM 4400 (text-figs. 5*f*, *g*, 6*b*). Specimen in counterpart referred by Moodie (1916) to *E. parvum* and by Gregory (1950) to *M. caudatum*. FMNH PR664 (text-figs. 4, 5*a*, *b*). An undescribed specimen in counterpart.

Localities and horizon. FMNH UR38 and USNM 4400 are from Mazon Creek near Morris, Grundy Co., Illinois. FMNH PR664 is from Peabody Coal Company Pit 11 spoil heap, Will-Kankakee Counties, Illinois. Horizon as for previously described material.

Diagnostic characters. As described above, these three specimens share a suite of characters with *A. grandiceps*, several of these characters being relatively rare in Palaeozoic temnospondyls but which also occur in *Branchiosaurus*. Despite a general similarity to *Branchiosaurus* based on primitive and larval features, these three specimens each share characters with the larger *Amphibamus* specimens which distinguish them from *Branchiosaurus*. These are as follows:

(i) Absence of hyobranchial ossifications. A negative and perhaps a weak character but the palates of all three specimens are clearly preserved (text-fig. 5*b*, *d*, *g*) and none of the specimens show signs of disintegration. The only dissorophid known to possess hyobranchial ossifications is *Micropholis stowi* from the Lower Triassic of the Karroo, none of the smaller Permo-Carboniferous dissorophids showing any trace of such structures. *Branchiosaurus* species possess hyobranchial ossifications which are usually visible in well-preserved specimens in palatal aspect.

(ii) None of the three specimens possess visible internal carotid foramina on the basal plate of the parasphenoid. In *A. grandiceps* there are no clear foramina but distinct grooves on either side of the base of the cultriform process (Watson 1940, fig. 4; this paper, text-fig. 3*b*). In *Branchiosaurus* the condition is variable but the foramina are usually prominent in small individuals comparable in size to the Mazon Creek larvae (Boy 1972, fig. 31*a*). In larger *Branchiosaurus* the foramina may be prominent holes or be replaced by deep grooves in the sides of the cultriform process (Boy 1972, figs. 31*b*, 32).

(iii) In FMNH UR38 and PR664 the ventral surface of the basal plate of the parasphenoid bears a patch of denticles on its anterior half. Post-metamorphic *A. grandiceps* also possess a patch of denticles in this area whereas *Branchiosaurus* species either possess no parasphenoid denticles at all (Boy 1972) or possess a small patch at the posterior end of the cultriform process (*B. humbergensis*, Boy 1978).

(iv) In FMNH PR664 and USNM 4400 the skull-tables can be seen to be extremely abbreviated antero-posteriorly and the supratemporals are about half the surface area of the parietals (text-fig. 5*a*, *f*). This corresponds to the condition in *Amphibamus*, particularly the ontogenetically younger specimen of *A. lyelli* (text-fig. 3*c*), more nearly than to the condition in *Branchiosaurus* (Boy 1972, fig. 24). FMNH UR38 appears similar in palatal aspect (text-fig. 5*d*) but in dorsal aspect, the supratemporals and parietals seem to be similar in surface area, giving the skull-table a more *Branchiosaurus*-like appearance (text-fig. 5*c*). This conflicts with the *Amphibamus*-like parasphenoid denticles and the longer quadrate ramus of the pterygoid (text-fig. 5*d*) and on balance I conclude that the specimen bears most resemblance to *Amphibamus* although it is less certainly assigned here than are the other two specimens.

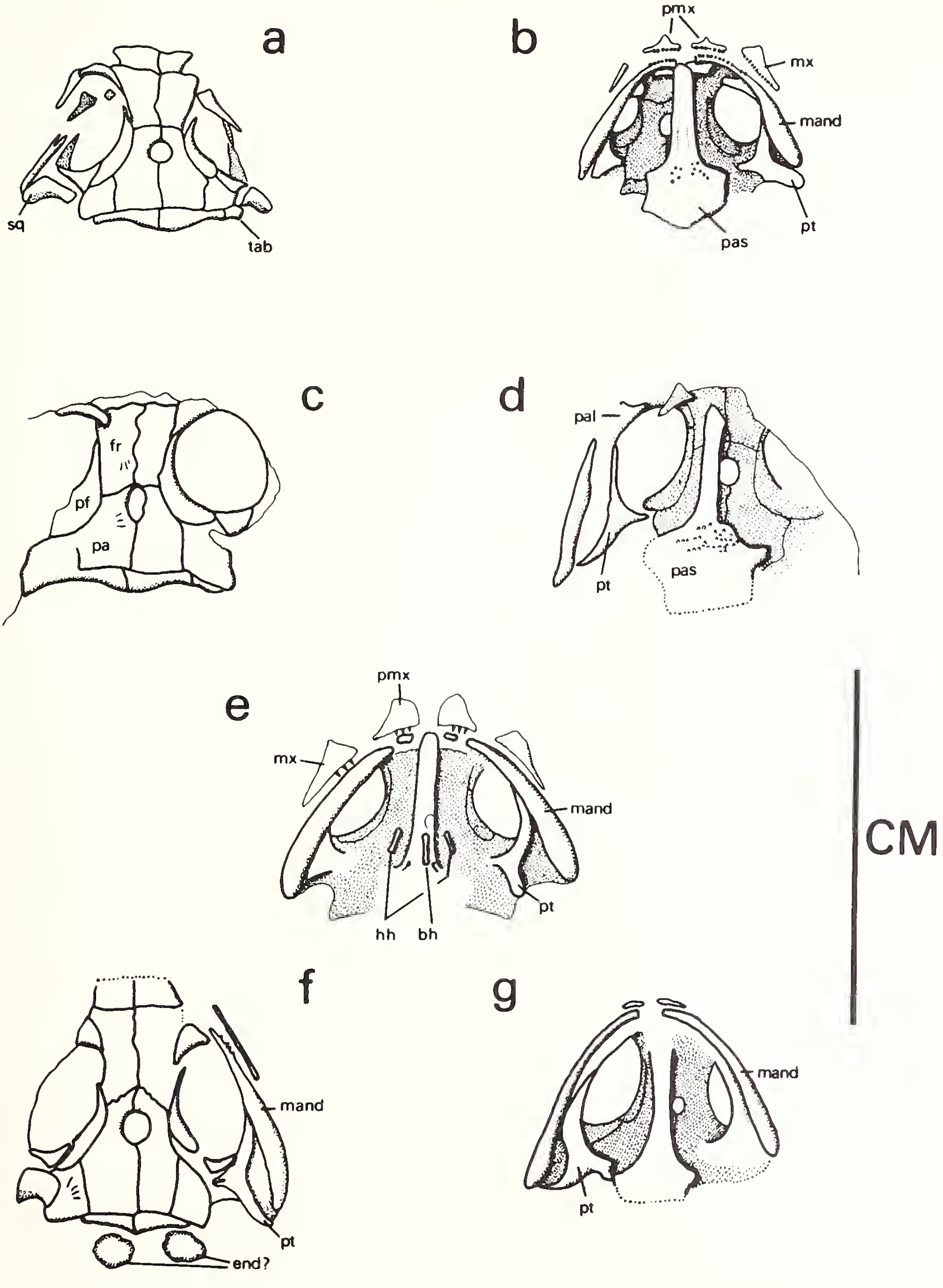
The above characters, which are all that the material permits, are all specific resemblances to *Amphibamus* rather than to *Branchiosaurus* and form the basis of this material being referred to *A. grandiceps*. I have not attempted to assess these character-states as being primitive or derived. As the attribution is to a slightly larger amphibian in the same assemblage, I believe the identification of typological similarities to be adequate.

Remarks. If these three specimens are accepted as aquatic larvae of *A. grandiceps*, they support Bolt's (1979, p. 549) conclusion that the previously recognized *A. grandiceps* specimens are post-metamorphic and that individuals underwent a relatively rapid metamorphosis between 7 and 14 mm mid-line skull length. During this metamorphosis the jaws elongated backwards, the suspensorium swinging back behind the level of the occiput with the result that the shallow larval otic notch grew into the deep semicircular otic notch characterizing post-metamorphic dissorophoids. The maxilla elongated posteriorly, as did the outer region of the squamosal. The vertebral centra presumably ossified at a slightly later stage, they are unossified in FMNH PR558 which has large notches in a skull about 12 mm long. The carpals and tarsals remain unossified in the larger *A. grandiceps*.

Among the characteristics of the *Amphibamus* larvae which have not been commented on so far, as they are not of immediate systematic significance, are the following:

(i) In FMNH PR664, external gills are visible (text-fig. 4*a*) indicating that the premetamorphic stage of *Amphibamus* was indeed aquatic. At least two pairs of external gills were present but the condition of preservation only permits the main filament of each gill to be identified and it is not possible to determine whether the gills were pinnate or not. No ceratobranchial dental

TEXT-FIG. 5. Skulls of larval dissorophoids from the Francis Creek Shale. (*a*, *b*) *Amphibamus grandiceps* Cope. FMNH PR664, dorsal and ventral counterparts. (*c*, *d*) *A. grandiceps* Cope. FMNH UR38, dorsal and ventral counterparts. (*e*) ?*Branchiosaurus* sp. YPM 803, in ventral aspect showing basihyal and hypohyals. (*f*, *g*) *A. grandiceps* Cope. USNM 4400, dorsal and ventral counterparts. Abbreviations: bh, basihyal; end?, endolymphatic sacs?; fr, frontal; hh, hypohyal; mand, mandible; mx, maxilla; pa, parietal; pal, palatine; pas, parasphenoid; pf, postfrontal; pmx, premaxilla; pt, pterygoid; tab, tabular.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ossicles are present and it is possible that such structures remained unossified in larvae of forms which became terrestrial while still small. As already described, such ossicles, probably functioning as gill rakers, are prominent in small aquatic temnospondyls (*Branchiosaurus*) and in the larvae of large aquatic temnospondyls which do not have them when adult (*Archegosaurus*, *Saurerpeton*). The adult *Amphibamus* was clearly terrestrial and had undoubtedly lost any gill-slits which the larva may have possessed.

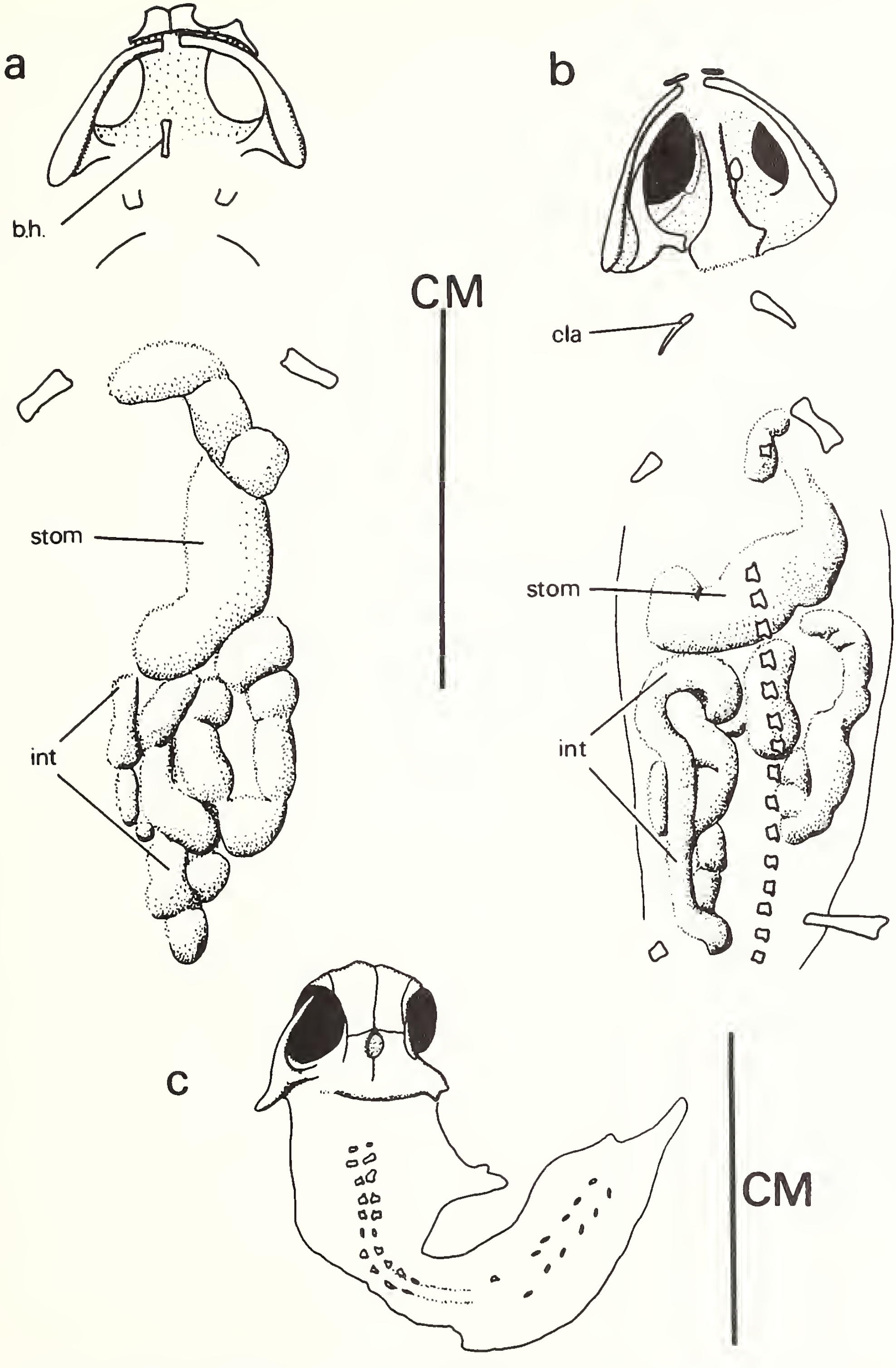
(ii) In USNM 4400 (text-fig. 5*f*), two calcareous lumps are present behind the occiput. Gregory (1950, fig. 9) appears to have interpreted one of these as the occiput itself. As noted by Boy (1974, p. 261), these correspond to structures occurring frequently in very small *Branchiosaurus* and appear to be endolymphatic calcium storage glands such as occur in the larvae of the living Anura.

(iii) In USNM 4400 (text-fig. 6*b*) the alimentary canal is unusually well represented as a series of casts of the stomach and intestine. These were described by Moodie (1916, p. 60) who also identified two impressions next to the cloacal region of the specimen as either glands or the posterior regions of oviducts. I cannot confirm this observation and it is unlikely that a larva would have possessed substantial oviducts.

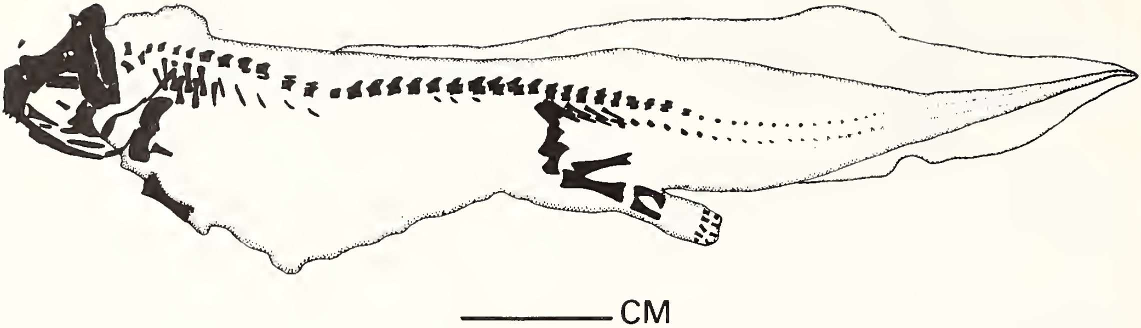
(iv) In FMNH UR38 most of the tail is visible (Moodie 1916, pl. 2). I have examined this specimen and the tail contains traces of at least twenty-five vertebrae, suggesting that either the tail of *Amphibamus* was substantially larger than depicted by Gregory (1950, fig. 6, 16 caudals) or alternatively, that some resorption of the tail took place at metamorphosis. No post-metamorphic *Amphibamus* has an unequivocally complete tail so the matter must remain unresolved although it is likely that a short-bodied, long-limbed terrestrial form such as *Amphibamus* did have a comparatively short tail.

In the larva FMNH PR664 (text-fig. 4*a*), the caudal vertebrae are presumably unossified, but the muscular portion of the tail can be identified as a heavily carbonized film. The tail has been compressed sideways and the two carbonized strips correspond to the epaxial and hypaxial muscles. Peripheral to the muscular portion of the tail is a smooth surface with a clearly demarcated edge and covered by a light carbonized film which represents the remains of a membranous caudal fin extending above and below the tail. Because the trunk of the specimen is dorso-ventrally compressed while the tail is laterally compressed, the tail must have been twisted through 90° during compression. The caudal fins, which appear to narrow anteriorly and to terminate just posterior to the base of the tail, probably extended further forwards, particularly the dorsal fin which could have extended anteriorly along the trunk without being detectable in this specimen. It may be noted that among the larvae of living European salamandrids which resemble this larva in general shape, the upland stream-dwelling larvae which live in running water (*Salamandra*, *Euproctus*) have slender fins restricted to the tail itself, whereas still-water larvae (*Triturus*, *Pleurodeles*) have deep caudal fins, the dorsal fin extending as far forwards as the pectoral region. As *Amphibamus* is associated with lowland coal-swamp pools and deltaic conditions, the larval tail fin is more likely to have been extensive like those of still-water salamandrid larvae and to have been imperfectly preserved in FMNH PR664 which superficially resembles a stream-dweller.

The Francis Creek Shale localities are not the only ones to produce small temnospondyls with well-preserved tail fins and mention might usefully be made of a previously undescribed specimen of *Branchiosaurus* which also shows an extensive tail fin. The general similarity of *Branchiosaurus* to larval *Amphibamus* has been noted above and may be indicative of relationship, as will be argued below. At the Autunian 'branchiosaur'-producing exposures at Odernheim in West Germany, specimens of *Branchiosaurus* are frequently preserved with the musculo-skeletal portion of the tail preserved as a carbonized film. Bulman and Whittard (1926) reconstructed *Branchiosaurus* from Odernheim with a short flattened tail two-thirds of the length of the trunk with only five ossified caudal vertebrae, based solely on the preserved musculo-skeletal portion of the tail as present in their material. Whittard (1930) and Boy (1972) had access to better specimens and were able to reconstruct *Branchiosaurus* with a longer tail terminating in a point and containing eleven to eighteen ossified



TEXT-FIG. 6. Entire specimens of larval dissorophoids from the Francis Creek Shale. (*a*) ?*Branchiosaurus* sp. YPM 802. (*b*) *Amphibamus grandiceps* Cope. USNM 4400. (*c*) Indeterminate larval dissorophoid, USNM 4319. Abbreviations: b.h, basihyal; cla, clavicle; int, intestine; stom, stomach.



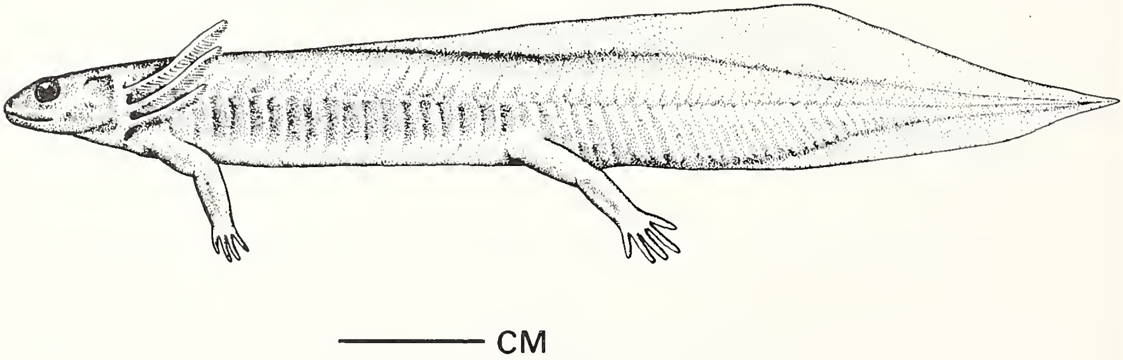
TEXT-FIG. 7. *Branchiosaurus* cf. *petrolei* (Gaudry). KC106 from Odernheim, Saarpfalz, West Germany. Specimen showing dorsal and ventral caudal fin membranes and terminal filament of tail.

caudal vertebrae. One specimen from Odernheim (KC 106 in text-fig. 7) has an exceptionally well-preserved tail in which not only are twenty-four ossified caudal vertebrae visible but there is also a terminal filament and substantial dorsal and ventral fins. The dorsal fin is deep and extends along the back whilst the ventral fin extends forwards almost to the cloaca. The restoration in text-fig. 8 is based on KC 106 (in which the head is somewhat smaller than average) and gives an indication of the true shape and size of the tail in *Branchiosaurus* and probably in larval *Amphibamus* as well. This shape and size of tail is consistent with the occurrence of *Branchiosaurus* in shallow lake deposits in the Saarpfalz intermontane basin and with *Amphibamus* in deltaic and coal-swamp pool deposits.

Family BRANCHIOSAURIDAE Frič 1883
Genus BRANCHIOSAURUS Frič 1876

Type species. *Branchiosaurus salamandroides* Frič 1876.

Diagnosis. The genus is diagnosed at length by Boy (1972, p. 39) and further described in a later paper (Boy 1978).



TEXT-FIG. 8. Restoration of *Branchiosaurus* based on specimen KC106.

?*Branchiosaurus* sp. indet.

Text-figs. 5*e* and 6*a*

Selected synonymy

1910 *Eumicrerpeton parvum* Moodie; p. 367, figs. 1–4.
1911 *Eumicrerpeton parvum* Moodie; p. 427, fig. 1.
1916 *Eumicrerpeton parvum* Moodie; p. 57, fig. 15*b*, *c*, pl. 3, figs. 1, 2.
1950 *Micrerpeton caudatum* Moodie; Gregory p. 857, fig. 8 *partim! non Moodie.*

Material. YPM 803 (text-fig. 5*e*). The type of Moodie's *E. parvum*, included by Gregory in *M. caudatum*. YPM 802 (text-fig. 6*a*). Referred to *E. parvum* by Moodie and to *M. caudatum* by Gregory.

Locality and horizon. Mazon Creek. Details as for *A. grandiceps.*

Remarks. These two specimens were first described by Moodie as a new species of branchiosaurid *E. parvum* and later reduced in synonymy with *M. caudatum* Moodie by Gregory (1950). Both specimens are small and poorly preserved but, as noted by Boy (1974, p. 261), both possess characters which suggest that their affinities lie with *Branchiosaurus* rather than with the *Amphibamus* material described above. These characters are:

(i) Possession of an ossified basihyal (YPM 803, 802) and ossified hypohyals (YPM 803).
(ii) Presence of prominent internal carotid foramina on the basal plate of the parasphenoid (YPM 803).
(iii) Absence of denticles on the ventral surface of the parasphenoid (YPM 803). I cannot confirm Gregory's observation of a patch of denticles on this specimen.

As described previously, the small specimens attributed to *A. grandiceps* do not possess hyobranchial ossifications or visible internal carotid foramina but do possess a denticle field across the anterior region of the base of the parasphenoid. Some of these specimens (FMNH PR664) are just as small as YPM 803 and 802, suggesting that these are size independent characters rather than ontogenetic differences. The attribution of YPM 803 and 802 to *Branchiosaurus* is necessarily tentative because of their poor preservation, but in such features as can be observed they correspond to *Branchiosaurus*. A possibility that cannot be excluded is that all the 'Mazon Creek larvae' belong to *Amphibamus* and that some are large premetamorphic aquatic larvae while others are small metamorphosing individuals which have acquired some *Amphibamus* palatal characters while still retaining gills (FMNH PR664). In this instance I think that this is less economical than referring the larvae to two taxa as they are typologically different at the same body size. Ultimately, collection of a larger sample of larvae would permit us to establish if more than one growth series is present, as Boy (1972) was able to do with the Odernheim assemblage of 'branchiosaurs'.

Although more precise determination is not possible, two further observations can be made. YPM 803 shows a prefrontal–postfrontal suture excluding the frontal from the orbit margin (text-fig. 5*e*) and also ossified ventral dermal scales, both of which are primitive characters within the genus *Branchiosaurus*. The prefrontal–postfrontal contact characterizes *B. salamandroides* Frič from the Westphalian D of Nýřany and Třemošná, *B. fayoli* Thevenin from the Stephanian of Commentry, and *B. dracyi* Boy (attributed to Milner) from the basal Autunian of Dracy St. Loup. Ossified dermal scales occur in small specimens, only in *B. salamandroides* and *B. fayoli*. The Mazon Creek material is thus comparable to *B. salamandroides* and *B. fayoli* in these features, but can neither be diagnosed as referable to any of the European species nor can it be separately diagnosed to justify the specific name *parvus*. Hence the material is simply identified as ?*Branchiosaurus* sp. indet.

Indeterminate dissorophoid larvae.

With so few characters distinguishing *Branchiosaurus* from *Amphibamus* larvae, it is inevitable that some of the smaller Francis Creek Shale larvae will be indeterminate. Two such are USNM 4319 (text-fig. 6*c*), described by Gregory (1950, p. 860) but not previously illustrated, and USNM 4432. USNM 4319 is undoubtedly referable to one of the above-described taxa but is not critically diagnostic.

ON THE RELATIONSHIP OF THE BRANCHIOSAURIDAE TO THE DISSOROPHIDAE

In recent years the families Branchiosauridae and Dissorophidae have been much studied, the former by Boy (1971, 1972, 1974, 1978) and the latter by Carroll (1964), DeMar (1966, 1968), and Bolt (1974*a*, *b*, 1977, 1979) and both families are now recognized as representing major radiations of small temnospondyls during the Permo-Carboniferous. The difficulties encountered during this study in differentiating larval *Amphibamus* from *Branchiosaurus*, even using derived characters, leads to the conclusion that branchiosaurids are more closely related to dissorophids than to any other family of temnospondyls and may even be more closely related to some dissorophids than to others. Boy (1978) has argued, I believe correctly, that branchiosaurids were either facultatively or permanently neotenous relatives of small terrestrial temnospondyls, exploiting plankton-feeding niches in the Autunian intermontane lakes. That their closest terrestrial relatives were the dissorophids is suggested by the following shared derived characters, some of which have already been itemized in the discussion of the identity of the 'Mazon Creek' larvae.

1. Centre of ossification of the jugal behind the level of the posterior edge of the orbit, with the jugal narrowing to a point anteriorly and never reaching the lachrymal. A dissorophoid character shared by the families Trematopidae, Micromelerpetontidae, Dissorophidae, and Branchiosauridae.
2. Extreme abbreviation of the skull-table, the distance from the posterior edge of the orbit to the tabular being about half the tabular–tabular width. Within the Dissorophoidea this character is restricted to the Branchiosauridae and the dissorophid genera *Amphibamus*, *Tersomius*, and *Doleserpeton*.
3. Reduction of the ectopterygoid. In most dissorophoids the ectopterygoid is a tiny bone bearing a 'tusk-pair', in branchiosaurids and *A. grandiceps* it is a slip of bone bearing a few small teeth and in *Doleserpeton* it appears to be absent.
4. Vomers bearing clumps or rows of teeth as well as or instead of 'tusks'. This also characterizes branchiosaurids, *Amphibamus*, *Tersomius*, and *Doleserpeton*.
5. Large otic notch, either deep or shallow, extending from the tabular to the quadrate, giving the squamosal an entirely concave posterior margin. A dissorophoid character occurring in all the dissorophoid families, although a more derived slit-like notch occurs in large, presumably adult, trematopids.
6. Pedicellate teeth? Pedicellate teeth are certainly present in several genera of dissorophid (Bolt 1977, 1979) and Boy has recently (1978) described structures resembling fused pedicels on the dentary of a large *Branchiosaurus*.
7. Presacral vertebral column reduced to twenty to twenty-one vertebrae. This is the normal condition in *Branchiosaurus* and occurs in some dissorophid genera (*Amphibamus*, *Cacops*).
8. Clavicles with narrow ventral blades and interclavicle reduced to a small rhomboidal plate usually smaller than one clavicle blade. Ossification of the interclavicle may be delayed in *Branchiosaurus*. This type of pectoral girdle occurs in dissorophids, branchiosaurids, and probably in trematopids but not in micromelerpetontids.
9. Long slender humerus with no supinator process. Occurs only in dissorophids and branchiosaurids.
10. Ribs reduced to very short straight structures. In small dissorophids such as *Amphibamus* and in branchiosaurids the ribs are much shorter than in any other small temnospondyl.
11. Although not strictly a shared derived character, it may be noted that in the Carboniferous *Branchiosaurus* species and in the Carboniferous dissorophid *Amphibamus* there is a prefrontal–postfrontal contact excluding the frontal from the orbit margin, whereas in the Permian *Branchiosaurus* and the Permian dissorophids the pre- and postfrontals are reduced and the frontal enters the orbit margin.

Characters 7–9 represent a functional complex of shorter trunk, longer limbs, and a pectoral girdle with reduction of the ventral dermal components. This is a complex that one might expect to find in small terrestrial amphibians such as the dissorophids but it also occurs in the manifestly aquatic *Branchiosaurus* and is one of the principal lines of evidence that has led Boy (1978) to deduce that *Branchiosaurus* is a neotenous relative of a terrestrial form. Because *Branchiosaurus* is clearly an aquatic form and smaller than most dissorophoids, those characteristics of the dissorophoids which are associated with large size and terrestriality need not be expected in a form in which metamorphosis does not appear to have occurred. Thus *Branchiosaurus* lacks the dorsal process on the quadrate, the posteromedial process on the quadratojugal and the lateral exposure of the palatine, all of which characterize the superfamily Dissorophoidea as originally conceived by Bolt (1969). The former two structures are probably intimately involved in the formation and support of a frog-like tympanum and need not be expected in an aquatic paedomorphic form in which the ontogenetic changes associated with terrestriality had been suppressed. The lateral exposure of the palatine likewise need not be expected in a tiny individual with very large orbits, this structure developing only as an 'infilling' of the cheek in larger skulls with relatively smaller orbits. The absence of such characters does not necessarily negate an immediate relationship between the branchiosaurids and the dissorophids. This is not to suggest that the Branchiosauridae and Dissorophidae are sister groups but rather that the Branchiosauridae represents a subgroup within the Dissorophidae as presently conceived, or in cladistic terms that the Dissorophidae is paraphyletic with respect to the Branchiosauridae. However, it is premature to suggest any change in classification at our present state of knowledge, for two reasons.

1. The Dissorophidae is widely agreed to be the group of Palaeozoic temnospondyls from which the Anura (and more controversially, the Urodela) evolved, and as such is almost certainly paraphyletic with respect to the Anura. In a strict cladistic classification, the Dissorophidae would be considered as a grade and fragmented into subgroups ranked according to their similarity to the Anura as manifested by derived skeletal characters. The Dissorophidae, as currently conceived, is made up of two major subfamilies of armoured forms, the Aspidosaurinae and the Dissorophinae which are not necessarily immediately related (DeMar 1966), plus several non-armoured forms of uncertain relationship. Bolt (1974*a*, 1977) has noted several of the potential ontogenetic complexities in systematizing these forms. Until we understand more fully the relationships of the dissorophids to one another and to the Anura, there is little purpose in attempting to determine the precise relationships of the Branchiosauridae.

2. The Branchiosauridae may be polyphyletic with respect to the Dissorophidae and may represent more than one lineage of paedomorphic forms. In both families the Carboniferous representatives retain a prefrontal–postfrontal contact while the Permian forms have the frontal entering the orbit margin. This may be convergence or coincidence or it may indicate that the Carboniferous *Branchiosaurus* is a neotenous relative of *Amphibamus* while the Permian *Branchiosaurus* is more closely related to the Permian dissorophids. Likewise, *Branchiosaurus humbergensis* Boy 1978, which is unusual in combining retention of parasphenoid denticles (otherwise unknown in *Branchiosaurus*) with an advanced skull construction, may represent a third *Branchiosaurus* lineage. In other words, it remains possible that the shared derived characters of *Branchiosaurus* are unrecognized larval dissorophid characters rendered more conspicuous in two or three independent lineages of large neotenous individuals. Alternatively the Branchiosauridae may prove to be a valid clade of neotenous dissorophids.

In conclusion, the Branchiosauridae is here suggested to consist of one or more lineages of paedomorphic dissorophids and hence to be more closely related to the Dissorophidae than to any other family of Palaeozoic temnospondyls.

THE FRANCIS CREEK SHALE TETRAPOD ASSEMBLAGE

Several recent discoveries and systematic reassessments of the tetrapods from the Francis Creek Shale permit a revised tetrapod faunal list to be compiled, updating that of Gregory (1950) and complementing the recent review of the Mazon Creek fish fauna provided by Bardack (1979). Further

Francis Creek Shale tetrapods are still known only from single specimens in private collections and are currently unpublished. The following listing refers only to published material in the collections of recognized institutions. It is also restricted to specimens which are determinate at some level.

Order TEMNOSPONDYLI

Dissorophidae: *Amphibamus grandiceps*—six 'adults', three larvae.
Branchiosauridae: ?*Branchiosaurus* sp. indet.—two specimens.
Saurerpetontidae: *Saurerpeton* cf. *obtusum*—one specimen.

This material has been listed and described in the systematic section of this paper.

Order BATRACHOSAURIA

Embolomeri *incertae sedis*: *Spondylerpeton spinatum*—one specimen.

A single specimen (YPM 793) consisting of two caudal vertebrae of a large embolomerous anthracosaur. This is the only large tetrapod fragment represented in the Francis Creek Shale assemblage. Panchen (1970) noted that the material is indeterminate at a generic level and that the binomen is a *nomen vanum* (more precisely a *nomen dubium*). Panchen initially assigned the specimen to the Archeriidae solely on the criterion of size but as the larger eogyrinid anthracosaurs had to pass through the archeriid size range during growth, this was hardly a valid taxonomic character used in isolation and Panchen later (1977) noted that it could equally belong to a leptophractine eogyrinid. The specimen appears to be indeterminate at family level and is here assigned to the Infraorder Embolomeri only.

Order AÏSTOPODA

Phlegethontiidae: *Aornerpeton mazonensis*—five specimens.

First described as *Phlegethontia mazonensis* by Gregory (1948). Subsequently, further specimens were described by Turnbull and Turnbull (1955), McGinnis (1967), and Lund (1978), the latter author raising the Francis Creek Shale material to separate generic status. The reported specimens are USNM 17079, MCZ 2204, FMNH PR291, FMNH PR400, and FMNH MCP501. A further specimen reported by Gregory (1950 p. 867) was reidentified as a lysorophid by Baird (1964)—see below.

Order NECTRIDEA

Urocordylidae: *Ptyonius marshii*—one specimen.

A single specimen (USNM 18125) first described by Gregory (1950, p. 866, fig. 10) as *Sauropleura* sp. but reidentified by Bossy (1976).

Order LYSOROPHIA

Lysorophidae: *Cocytinus* sp.—one specimen.

A single specimen (USNM 4313) first described by Gregory (1950, p. 867) as a specimen of *Phlegethontia* but reidentified by Baird (1964, p. 14, note 7) as *Cocytinus*.

Order MICROSAURIA

Family *incertae sedis*: unnamed specimen.

The only specimen (FMNH PR981) first described by Carroll and Gaskill (1978, p. 134). In their monograph, Carroll and Gaskill cautiously refer this specimen to the Hyloplesiontidae but note that because of poor preservation of the skull and manus, there is nothing to preclude assignment of this specimen to the tuditanomorph microsaur families Tuditanidae or Hapsidopareiontidae. The specimen, though of inherent interest, is thus strictly indeterminate at family level and I am treating it as such.

Order CAPTORHINOMORPHA

Family Protorothyrididae: *Cephalerpeton ventriarmatum*—one specimen.

The only specimen (YPM 796) was recently redescribed by Carroll and Baird (1972). It is probably a juvenile animal.

The above-listed material makes up a small sample of twenty-two specimens, an insignificant number in relation to the thousands of non-tetrapod specimens collected from the Francis Creek Shale concretions. The tetrapods are clearly transported erratics which do not relate directly to the environment of preservation but which may provide some information about the neighbouring terrestrial and freshwater environments. With the identification of further specimens, the Francis Creek tetrapod assemblage bears an increasing resemblance to the contemporary tetrapod assemblage from Linton, Ohio, but is not simply a smaller sample of an identical assemblage as at least two filters appear to have operated. One such filter apparently controlled the size of the preserved, or at least the collected material, as only one Francis Creek Shale tetrapod fossil is a fragment of a large animal. The others are all remains of animals less than 20 cm long. Richardson and Johnson (1971, p. 1230) note that the larger fish are also known only from fragments, some of which are from associated skeletons and they suggest that the larger vertebrates were buried intact and that complex nodules formed around them which broke up on re-exposure. However, the scarcity of described fragments of large tetrapods suggests that they may have been rarely preserved in the Francis Creek Shale, either because of the effects of current sorting of corpses or because the deltaic system was predominantly inhabited by small tetrapods. The second filter has operated in such a way that, although the range of tetrapod taxa resembles a small sample of the contemporary assemblage from Linton, Ohio, at least at the family level, the relative numbers of the different forms are quite distinct. This is not an observation on which great weight can be put because of the small size of the sample and the certainty that it is made up of erratics. Nevertheless, the relative numbers of tetrapod types present suggest that the Francis Creek Shale tetrapod assemblage is not just a small sample of a typical coal-swamp pool assemblage such as those from Linton or Nýřany. In a recent reassessment of the contemporary Nýřany assemblage (Milner 1980*b*), I interpreted that large assemblage of tetrapods from a small lake in a swamp-forest as comprising three different tetrapod associations. These were: an open water–lacustrine association characterized by eogyrinids and loxommatids; a terrestrial–marginal association characterized by many families including dissorophids, phlegethontiids, gymnarthrid, tuditanid and hapsidopareiontid microsaurs, and protorothyridid (romeriid) reptiles; and, thirdly, a swamp pool association characterized by ophiderpetontids, urocordylids, and the larvae of temnospondyls and microsaurs. Using the same family-to-association assignments as for the Nýřany and, by analogy, the Linton faunas, the Francis Creek Shale assemblage appears to contain:

One open water–lacustrine specimen—the embolomere *Spondylerpeton*.

Twelve terrestrial–marginal specimens—the adult *Amphibamus*, *Aornerpeton*, *Cephalerpeton*, and the microsaur.

Eight swamp pool specimens—the larval *Amphibamus*, *Branchiosaurus*, *Saurerpeton*, and specimens of *Ptyonius* and *Cocytinus*.

These relative numbers suggest that the Francis Creek Shale tetrapods derive as significantly from a terrestrial association as from a swamp pool association, unlike the Nýřany tetrapods, over 75% of which appear to derive from the swamp pool in which they were preserved. The conclusion that slightly over half of the Francis Creek Shale tetrapods, although erratics, were probably terrestrial, corroborates the observation of Johnson and Richardson (1966, p. 627) that the Braidwood fauna contained 85% terrestrial species, 11% fresh- or brackish-water species, and 4% marine species. These high representations of terrestrial forms are consistent with the interpretation that the Francis Creek Shale assemblages are the product of an active deltaic system subject to occasional channel diversions and river floods (Shabica 1979). Of the known tetrapods, the embolomere, as a probable open-water form, may have lived in the delta river itself. The small terrestrial- and pool-dwelling forms were probably inhabitants of the deltaic lobes and were flushed into the sea along with considerable quantities of mud, either by a storm-surge (Richardson and Johnson 1971) or more probably by a river flood (G. C. Baird 1979). The limited diversity of inferred terrestrial forms (*Amphibamus*, *Aornerpeton*, and *Cephalerpeton*) may represent a small association of specialized forms adapted to life on the levees of the delta fan lobes, while the pool-dwellers and larvae inhabited freshwater pools in the delta.

No observations of geographical significance appear to be possible, except that the closest resemblance of the assemblage is to that from Linton, Ohio. Except for the Branchiosauridae, all the tetrapod families recorded from the Francis Creek Shale occur at Linton, whereas the Saurerpetontidae, Lysorophidae, and *Ptyonius* do not occur in the Nýřany assemblage. Only *Branchiosaurus* is a specific similarity to the Nýřany assemblage, but although this genus is unrecorded from Linton, it is described from the Stephanian of the Tristate area (Romer 1939). Thus the Francis Creek Shale tetrapod assemblage is geographically entirely consistent with other contemporaneous coal-swamp tetrapod assemblages from North America.

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AN EVOLUTIONARY SEQUENCE IN *ARATRISPORITES* MIOSPORES FROM THE TRIASSIC OF QUEENSLAND, AUSTRALIA

by N. J. DE JERSEY

ABSTRACT. Specimens of *Aratrisporites*, a miospore genus of probable lycopsid affinity, are common in some palynofloral assemblages of Early Triassic age, from the Rewan Formation of the Bowen Basin, Queensland. Study of numerous specimens from a sequence about 1710 m. thick supports the view that *A. tenuispinosus* developed, by increase in spine dimensions, from *A. wollariensis*. The observed development of this evolutionary sequence favours quantum speciation, rather than a gradualistic process, as the change from one species to the other takes place over a relatively short stratigraphic interval. It is unusual, in the palynological record, for specimens, showing an evolutionary transition between species, to be observed; reasons for their occurrence in this case are suggested.

ARATRISPORITES Leschik emend. Playford & Dettmann, 1965 is a genus of two-layered, monolete miospores. The spore wall is cavate and consists of an outer structured layer loosely enveloping but proximally attached to a homogeneous inner layer. The outer layer is finely patterned and has sculptural elevations such as grana, coni, spinulae, spinae, and saetae. The monolete laesura is enclosed within elevated lips. There is strong evidence for a lycopsid affinity for the genus; Balme stated (1970, p. 351) 'spores of the *Aratrisporites* type have been reported from four Triassic lycopsid fructifications: *Lycostrobus scotti* (Nathorst), and recently from three species of *Cylostrobus* Helby and Martin, from the Narrabeen Group in New South Wales, Australia (Helby and Martin 1965). Such unusual morphological characters are combined in these spores that the presence of *Aratrisporites* in an assemblage may be confidently assumed to indicate a lycopsid element in its parent flora.'

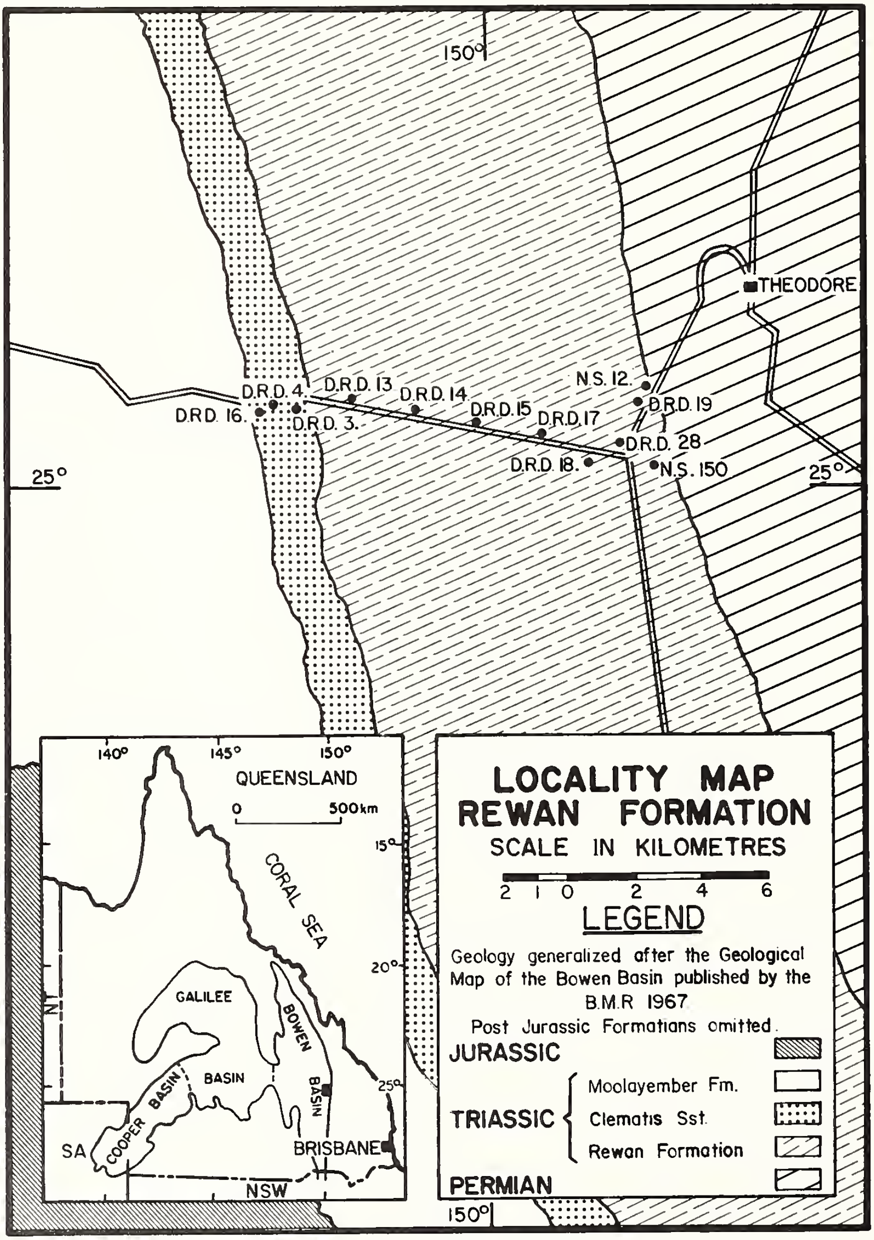
Species of *Aratrisporites* are characteristic and widespread components of Triassic miospore assemblages. There are numerous records of the genus in European, Asian, and Australian palynofloras; both Balme (1970, p. 445) and de Jersey (1979, pp. 35, 36) have discussed the biostratigraphic significance of its first appearance. In Australia *Aratrisporites* is widely distributed in Early Triassic palynofloras. In the Bowen Basin, Queensland, two apiculate species, *Aratrisporites wollariensis* Helby, 1967 and *A. tenuispinosus* Playford, 1965, are relatively persistent components of assemblages from the middle and upper parts of the Rewan Formation and comprise from 20 to over 80% of the total miospore population in some of the assemblages recorded (de Jersey 1970, fig. 3).

As interpreted here (see also de Jersey 1970, pp. 11, 12, pls. 3, 4) *A. wollariensis* and *A. tenuispinosus* are similar in size and basic construction, but differ in the size and robustness of the apiculate projections. In *A. wollariensis* these comprise coni, grana, and spinae from 0·5 to about 2·0 μm in length, while in *A. tenuispinosus* the spinae range from about 2·0 to 6·0 μm in length. As the first appearance of the latter species is significantly higher in this Rewan succession than that of *A. wollariensis* (de Jersey 1970, fig. 3), there is biostratigraphic evidence for suggesting an evolutionary development of one species from the other, by increase in the size of the spinose projections. In this paper, the results of a re-examination of the Rewan material, undertaken, first, to reassess evidence for separating the two species and, secondly, to explore the possibility of an evolutionary relationship between them, are recorded.

[Palaeontology, Vol. 25, Part 3, 1982, pp. 665–672, pl. 65.]

STRATIGRAPHIC SETTING

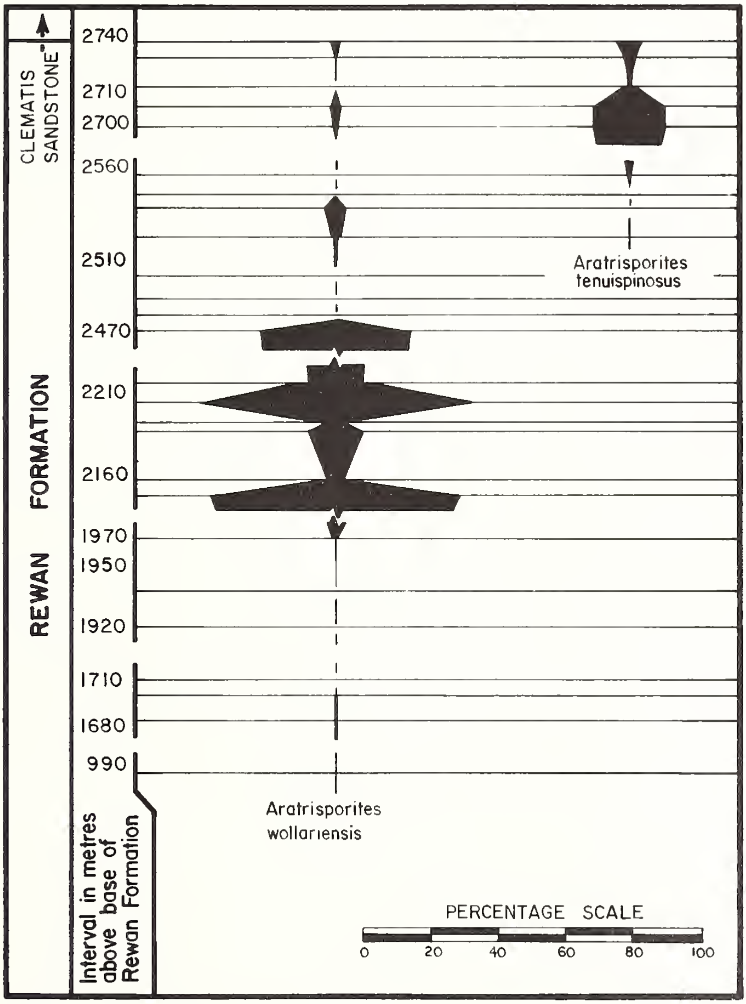
The material studied came from the eastern side of the Bowen Basin, one of three large basins of Permian and Triassic sediments in Queensland (text-fig. 1). The section sampled is located east of the axis of the Mimosa Syncline, where the Rewan Formation attains its thickest development, of approximately 2750 m (de Jersey 1970, pp. 1–3). The initial study of miospore distribution in this sequence (de Jersey 1970) was based on samples from a series of stratigraphic boreholes (text-fig. 1), sections from which were assembled to provide a composite stratigraphic section (de Jersey 1970, fig. 2). As the boreholes were relatively shallow (about 100 to 130 m) there



TEXT-FIG. 1. Map (based on de Jersey 1970, fig. 1), showing locations of stratigraphic boreholes in the eastern Bowen Basin of Queensland.

are gaps in the composite sequence, especially in the lower part of the Formation; there was, however, better coverage of the middle and upper parts of the sequence, which provided the material recorded in this paper.

The Rewan Formation is of continental origin; it consists dominantly of mudstone and siltstone, with minor sandstone and conglomerate beds and is virtually devoid of coal—a feature which differentiates it readily from the underlying Permian coal measures. A striking feature is the presence of 'red-beds', consisting dominantly of chocolate mudstone, which form a prominent part of the sections penetrated in D.R.D. 15, D.R.D. 17, D.R.D. 18, and D.R.D. 28 (text-fig. 1). Red-beds are absent, or of only minor significance in the other borehole sections. The effect of facies on the miospore assemblages has been demonstrated by comparison of palynofloras from sediments interbedded with red-beds, with those from sediments in sections devoid of red-beds. Marked differences in composition of the assemblages were observed (de Jersey 1970, pp. 22–24) with *Aratrisporites* present in only small proportions in the middle part of the sequence, in sediments interbedded with red-beds, but occurring in relatively high percentages, as shown above the 1950 m level in text-fig. 2, in the upper part of the Formation, which is devoid of red-beds.



TEXT-FIG. 2. Percentage distribution of *Aratrisporites wollariensis* and *Aratrisporites tenuispinosus* in miospore assemblages from the middle and upper Rewan Formation (based on de Jersey 1970, fig. 3). Horizontal lines represent sample levels; gaps in the chart represent gaps in coverage of borehole sections.

In a comprehensive account of lithostratigraphy and sedimentation in the Bowen Basin (Jensen 1975), two units of formational rank were distinguished in the Rewan succession of the central and western portions of the Basin and the Rewan Formation was raised to the status of a Group. However, those units are not recognized in subsurface sections in the south-eastern part of the Basin (Jensen 1975, p. 60), which includes the area considered in this paper and the designation Rewan Formation has therefore been retained for the sequence considered here.

The age of the Rewan Formation has been discussed by de Jersey (1970, pp. 26, 27; 1979, pp. 34–36) and Foster (1979, pp. 129–139) on the basis of comparison of palynofloras from that formation with others from Upper Permian–Lower Triassic successions, dated by marine faunas. There is some uncertainty where the Permian–Triassic boundary should be located, within the lower part of the Rewan Formation; however, there is strong evidence for regarding the middle and upper portions of the sequence (containing *Aratrisporites*) as Early Triassic in age.

SEQUENCE OF POPULATIONS INDICATING DEVELOPMENT OF *ARATRISPORITES TENUISPINOSUS* FROM *ARATRISPORITES WOLLARIENSIS*

The percentage distribution of *A. wollariensis* and *A. tenuispinosus* in the Rewan Formation is shown in text-fig. 2 (after de Jersey 1970). Re-examination of this material has been carried out by morphological study of numerous specimens from various levels in the section covered by text-fig. 2, supplemented by quantitative studies of size distribution of the spines. Data from the quantitative studies are based on measurements of the maximum spine length at the equator of 100 well preserved, suitably oriented specimens, from four assemblages in which specimens of *Aratrisporites* are abundant and well preserved. The results of these quantitative studies are summarized in Table 1.

TABLE 1. Size distribution of spine lengths in specimens of *Aratrisporites* from the Rewan Formation

Sample (borehole, depth)	Approximate interval in metres above base of Rewan Formation	Size distribution of maximum spine lengths (in μm, based on 100 specimens)				Representative illustration in pl. 65
		<1	1–2	2–4	4–6	
D.R.D. 3, 34·57 m	2700		2	73	25	
D.R.D. 3, 38·89 m	2700	1	4	50	45	Figs. 1–3
D.R.D. 14, 44·35 m	2200		95	5		Fig. 7
D.R.D. 14, 89·79 m	2150	1	98	1		Figs. 6, 8

It is clear that over an interval of 550 m there is a marked change in the morphological distribution of the assemblages, indicated by an approximate doubling of the average maximum spine length. The differences between the lower and upper assemblages become even more apparent with detailed study

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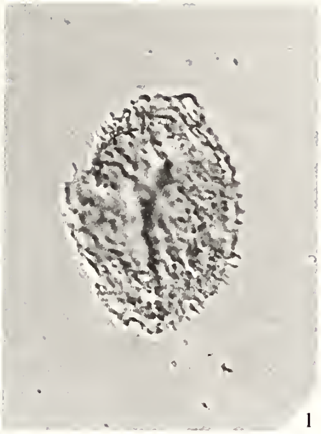
EXPLANATION OF PLATE 65

All specimens approximately ×1000, equatorial focus, differential interference contrast; for details of the provenance of figured specimens see Appendix. The numbers in metres recorded after the species indicate the approximate interval above the base of the Rewan Formation, and are arranged on the plate in lines of similar depth.

Fig. 1. *Aratrisporites wollariensis* Helby, 1967, 2700 m.
Figs. 2, 3. *Aratrisporites tenuispinosus* Playford, 1965, 2700 m.
Figs. 4, 5. Specimens transitional between *A. wollariensis*, and *A. tenuispinosus*, 2520–2540 m.
Figs. 6–8. *Aratrisporites wollariensis* Helby, 1967, 2150–2200 m.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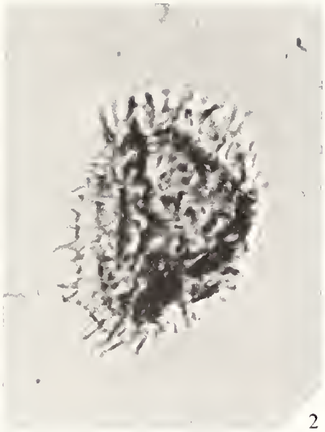
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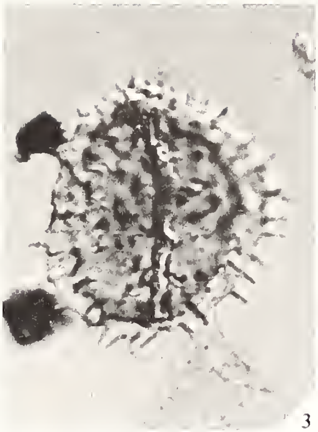
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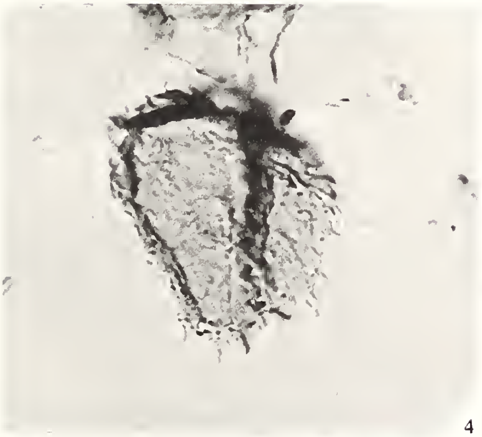
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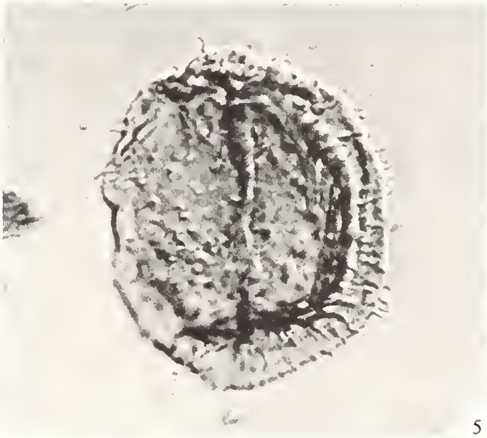
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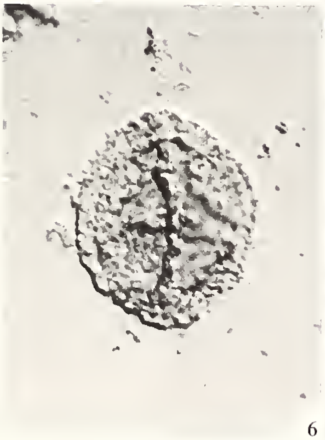
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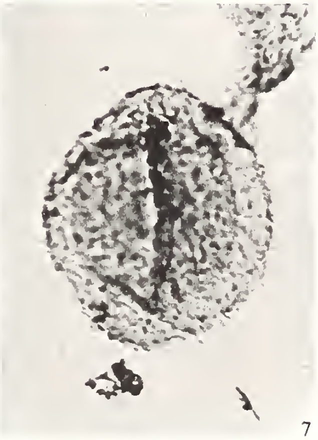
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DE JERSEY, *Aratrisporites*

of the specimens, from which it is evident that in the two lower assemblages specimens with maximum spine lengths over 2 μm have only a small proportion of longer spines, and are regarded as extreme variants of *A. wollariensis*. In the two upper assemblages, in specimens with spines of maximum length greater than 2 μm, the spines tend to be uniformly longer.

Specimens representative of the populations used for these measurements are illustrated in Pl. 65 with the spine length increasing from left to right, for each of the stratigraphic levels considered. In terms of described species, specimens represented by fig. 1 and figs. 6–8 (Pl. 65) conform in all significant diagnostic features to the description and figures of *A. wollariensis* Helby, 1967 (Helby 1967, p. 67, pl. 1, figs. 17–19). Specimens represented by figs. 2 and 3 conform in all significant features to the description and figures of *A. tenuispinosus* Playford, 1965 (Playford 1965, pp. 196, 197, pl. 11, figs. 3–7).

The marked differences between the lower and upper populations support the view that *A. wollariensis* and *A. tenuispinosus* should be retained as separate species, and that the older assemblages (from 2150 to 2200 m above the base of the formation) containing only *A. wollariensis* are replaced by a mixed population, containing both species, in assemblages from about 2700 m above the base of the formation. In the intervening section, comprising the interval between assemblages containing abundant *A. wollariensis* (2150 to 2470 m above the base of the formation) and those containing abundant *A. tenuispinosus* (2700 to 2740 m above the base of the formation), quantitative studies of spine lengths have not been possible because of the relative scarcity of *Aratrisporites* in all the material examined. However, the combined population from 2520 to 2540 m above the base of the formation contains specimens which are intermediate in length and general robustness of the spines, between *A. wollariensis* and *A. tenuispinosus* (Pl. 65, figs. 4, 5). The transition between the species is evident in comparing figs. 7, 8 (2150 to 2200 m), figs. 4, 5 (2520 to 2540 m), and figs. 2, 3 (2700 m). It is concluded that *A. tenuispinosus* developed, by increase in spine dimensions, from *A. wollariensis*.

With regard to *in situ Aratrisporites* (from microsporangia), spores morphologically similar to *A. tenuispinosus* have been described from three species of *Cylostrobus*, a genus of lycopsid cones, by Helby and Martin (1965). The relatively close similarity in morphology of the microspores from the three species (*Cylostrobus sydneyensis*, *C. major*, and *C. grandis*) is indicative of conservatism in microspore characters, in contrast to differences in the other features of these species. The evidence, recorded above, for derivation of *A. tenuispinosus* from *A. wollariensis* is thus suggestive of the derivation of these three species of *Cylostrobus* from a lycopsid species which produced microspores of the *A. wollariensis* type. The three species of *Cylostrobus* were recorded from the upper part of the Narrabeen Group, in the Sydney Basin. This part of the Narrabeen Group is regarded, on palynological evidence, as being approximately equivalent in age to the upper Rewan Formation.

CONCLUSIONS: EVOLUTIONARY SIGNIFICANCE

The value of palynological evidence in interpreting the mechanism of evolution was discussed by Professor W. G. Chaloner in a lecture to the Fifth International Palynological Conference. His remarks are so relevant to the current study that they are quoted almost in their entirety. He stated (Chaloner 1980, p. 7): ‘the fossil record of both plants and animals is singularly lacking in evidence of gradual evolutionary change. A statement from the first edition of “The Origin of Species” summarises the situation now as aptly as when Darwin published it: “Geological research, though it has added numerous species to existing and extinct genera, and has made the intervals between some few groups less wide than they otherwise would have been, yet has done scarcely anything in breaking down the distinction between species, by connecting them together by numerous fine, intermediate varieties, and this not having been effected, is probably the gravest and most obvious of all the many objections which may be urged against my views”. Now, a hundred years later, this objection is still with us. Wherever we have long successions of plant-bearing deposits—the Coal Measures, the middle Jurassic of Yorkshire—there is a limited amount of change—of species and genera coming and going, but very little evidence of gradual change. In the current jargon of palaeontology the evidence favours a punctuational process rather than a gradualistic one. The *incompleteness* of the macroplant record, which is, of course, what Darwin invoked for the lack of evidence of gradual change in the animal fossil record, was, I suppose, accepted by most palaeobotanists. But with the surge of palynology from the 1950's onwards, we came to have a much fuller and more continuous record of spores than we ever had from the more discontinuous occurrences of plant macrofossils. Many of us hoped that somehow we would see behind the scenes, and catch one species turning into another. And yet the record of evolutionary change remained as discontinuous as ever. Spore species through the Carboniferous Coal Measures show no more sign of evolutionary drift, of one species "turning into another" than do the macrofossils.

We have to conclude that the plant population which is involved in the process of relatively rapid change is very small, the "bottleneck" process of quantum speciation, so convincingly advocated by Steven Stanley.'

If the Rewan sequence recorded here is considered in relation to gradualistic and punctuational processes of evolution, it provides evidence favouring the latter. Over a relatively long interval, between 990 and 2470 metres above the base of the formation, populations of *A. wollariensis* do not show significant changes in spine morphology. The abundance of specimens of the species at some horizons within this interval enables this lack of change to be clearly demonstrated. Coincident with reduction of the species to low proportions in the assemblages, presumably as a result of adverse conditions, specimens with larger spines appear between 2520 and 2540 metres above the base of the formation. This relatively rapid change, at a time when the species is reduced to quite minor proportions of the assemblages, can be related to Mode D, or quantum speciation of Stanley (1979, pp. 26–28), whereby rapidly divergent speciation occurs by way of a very small population. Higher in the formation, between 2560 and 2740 metres above its base, there is a further increase in spine length which warrants differentiation of a separate species, *A. tenuispinosus*. Stanley (1979, figs. 2–8 (D)) indicated that the new and the pre-existing species would coexist, and both *Aratrisporites* species are found at the higher levels in the Rewan succession.

The question that remains to be answered is why an intermediate stage, of one species 'turning into another', has been observed in this particular case. It can only be suggested that conditions in this case are exceptionally favourable. A long, continuous succession, reasonably well sampled, is available. The samples have yielded abundant, well-preserved miospores, and the evolutionary change occurs in a morphological feature that is readily observed and easily measured. Perhaps the most important factor of all is that the two species are so abundant at lower and upper levels that the size of the 'bottleneck' between them may be appreciably greater than usual, so that indications of it are observed in this case.

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APPENDIX

Provenance of specimens figured in Pl. 65

Specimens listed below are all on microslides in the palynological collection of the Geological Survey of Queensland, Brisbane. Stage co-ordinates are those of a Carl Zeiss GFL Microscope; the reference point refers to the lower right-hand corner of the cover glass, when the slide is inserted with the label to the observer's left.

Figure no. in Pl. 65	Species	Slide no.	Stage co-ords.	Reference point co-ords.	Sample locality (borehole, depth)
1	*A. wollariensis*	S1558	12·7, 94·2	22·7, 85·0	D.R.D. 3, 38·89 m
2	*A. tenuispinosus*	S1559	11·7, 87·6	22·8, 84·3	D.R.D. 3, 38·89 m
3	*A. tenuispinosus*	S1559	9·3, 93·5	22·8, 84·3	D.R.D. 3, 38·89 m
4	Transitional between *A. wollariensis* and *A. tenuispinosus*	S1584	21·2, 95·2	22·7, 83·5	D.R.D. 13, 52·58 m
5		S1584	5·7, 84·4	22·7, 83·5	D.R.D. 13, 52·58 m
6	*A. wollariensis*	S1623	16·7, 89·4	22·5, 85·1	D.R.D. 14, 89·79 m
7	*A. wollariensis*	S1640	11·5, 100·0	22·8, 85·9	D.R.D. 14, 44·35 m
8	*A. wollariensis*	S1624	16·7, 90·0	22·1, 82·0	D.R.D. 14, 89·79 m

THE TAXONOMIC STATUS OF THE MIOCENE HORSE GENUS *SINOHIPPUS*

by ANN FORSTEN

ABSTRACT. The large Asiatic anchitheriine, *Sinohippus zitteli*, is discussed and compared with some other Old and New World anchitheriines.

THE taxonomic history of *Sinohippus zitteli* has been a thorny one. Schlosser (1903, pp. 76–78; Taf. III. 6, 8–12) originally described *Anchitherium zitteli* on isolated teeth, probably from the 'Pontian' Red Clays of Shansi, China. Osborn (1918, p. 203) referred *A. zitteli* to the New World genus *Hypohippus* Leidy. Following Osborn, Schlosser (1924, p. 68; Taf. V. 10) referred material from Olan Chorea, Mongolia, to *H. zitteli*. Zdansky (1935, pp. 17–20; Taf. I. 4, II. 1) described additional material from Loc. 31, Shansi, but did not assign it to genus or species. Finally, Zhai (1962) erected a new genus, *Sinohippus*, for this large Asiatic anchitheriine.

DESCRIPTION

Skull and teeth

Osborn (1918, p. 203) did not give particular reasons for referring *zitteli* to *Hypohippus*, but listed eleven characters thought to characterize the genus *Hypohippus*, including *zitteli*. Of these some do characterize *zitteli*, at least with amendments, while others do not.

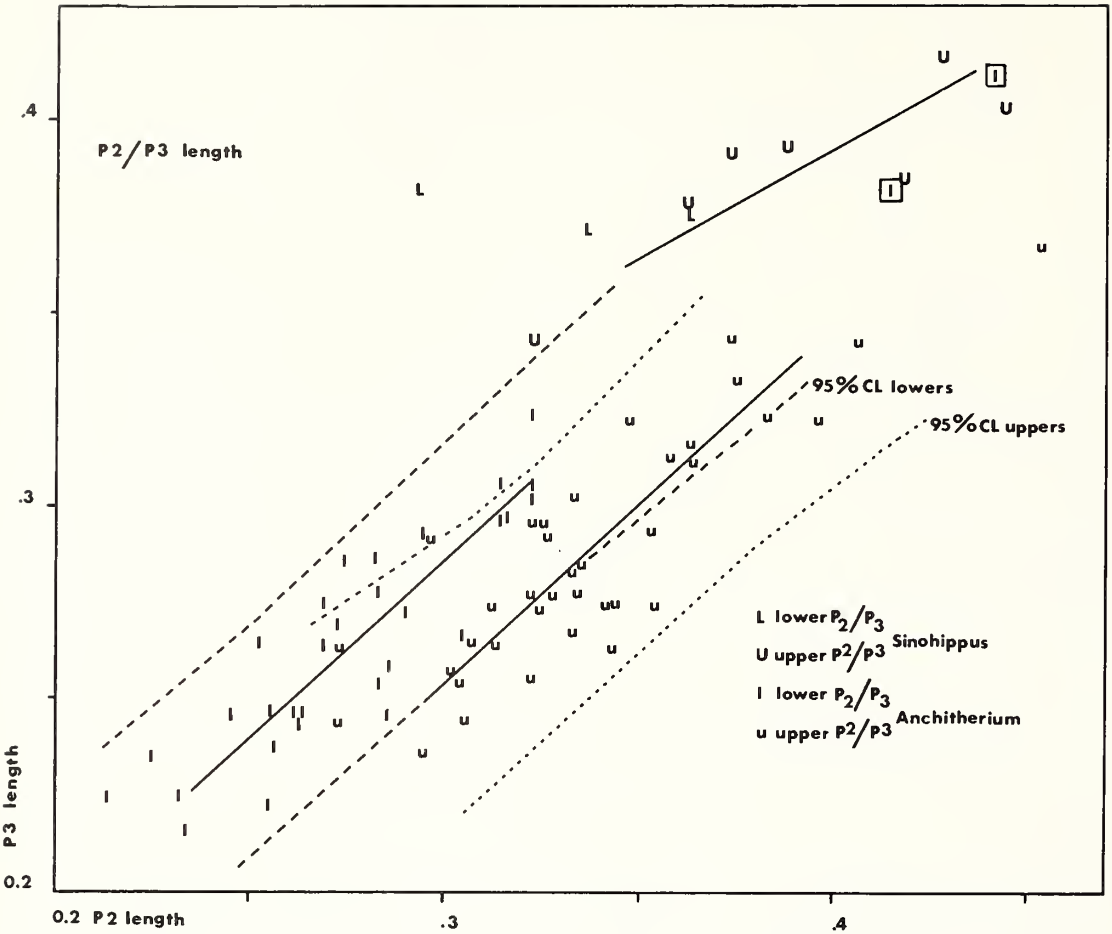
The most marked difference between *zitteli* and *Hypohippus* relate to the development of the preorbital fossa. As set down for *Hypohippus* in Osborn's characters 7 and 8: 'Lacrymal fossa deep, narrow, and superior in position' and 'No malar fossa'. In a skull of *S. zitteli* (AMNH 38-L-272) from Ma Chi Lieu Kou, north-west Shansi, the fossa is very wide and large, lacking sharp boundaries except posteriorly; it thus resembles the fossa of Old World *Anchitherium* (e.g. Kowalevski 1873, pl. III. 50, and crushed skull from Sansan, Paris, 158), rather than that of New World *Hypohippus* (e.g. *H. osborni*, *H. affine*).

Of the tooth characters common to *Sinohippus* and *Hypohippus* Osborn (1918, p. 203) mentioned the reduced M3/3. In post-Barstovian *Hypohippus* both the anterior (P2/2) and posterior (M3/3) peripheral cheek teeth are reduced relative to their neighbours (P3/3 and M2/2) (Forsten 1973, figs. 1–4). *Sinohippus* resembles *Hypohippus* in these regards (text-figs. 1–2). In Old and New World *Anchitherium* the relative size and/or growth of the peripheral teeth is different (Forsten 1973, figs. 1–4; this paper text-figs. 1–2). The alleged reduction of the posterior part of M1–2/1–2, with respect to the anterior part of P3–4/3–4, which according to Zhai (1962, pp. 54–55) distinguishes *Sinohippus*, is not confirmed by my data. The shape of the intermediate premolars and molars of *Sinohippus* is the same as that of corresponding teeth of *Anchitherium* and *Hypohippus*. In all anchitheriines the trigonid is narrower than the talonid in the premolars, while the opposite is true of the molars; this in fact allows identification (Forsten 1970, pp. 4–5).

Neither do the other tooth characteristics listed by Zhai, e.g. well-developed styles, little angulated metaloph, and elongated teeth, differentiate *Sinohippus* from *Hypohippus*. With increase in size, the lower cheek teeth of *Sinohippus* do indeed increase slightly faster in length than in anterior breadth (l/b = 0·968), but in the upper cheek teeth breadth increases faster than length (l/b = 1·277). The teeth are thus not particularly elongated. The morphology of the cheek teeth of *Sinohippus* differs little from that in *Hypohippus*, except that in P^2 the protoloph is usually quite short, often with increased wear connecting to the paracone instead of to the ectoloph, and the hypoconulid of the lowers is reduced. Cingula are developed as in most *Hypohippus* (Osborn 1918, p. 203).

As in *Hypohippus*, shear along the crests of the teeth was enhanced in *Sinohippus*. There was vertical shear along the ectoloph, followed by shear along the metaloph parallel to occlusal motion resulting in vertical, wedge-shaped wear surfaces along the lophs (e.g. AMNH 33-L-278).

[Palaeontology, Vol. 25, Part 3, 1982, pp. 673–679.]

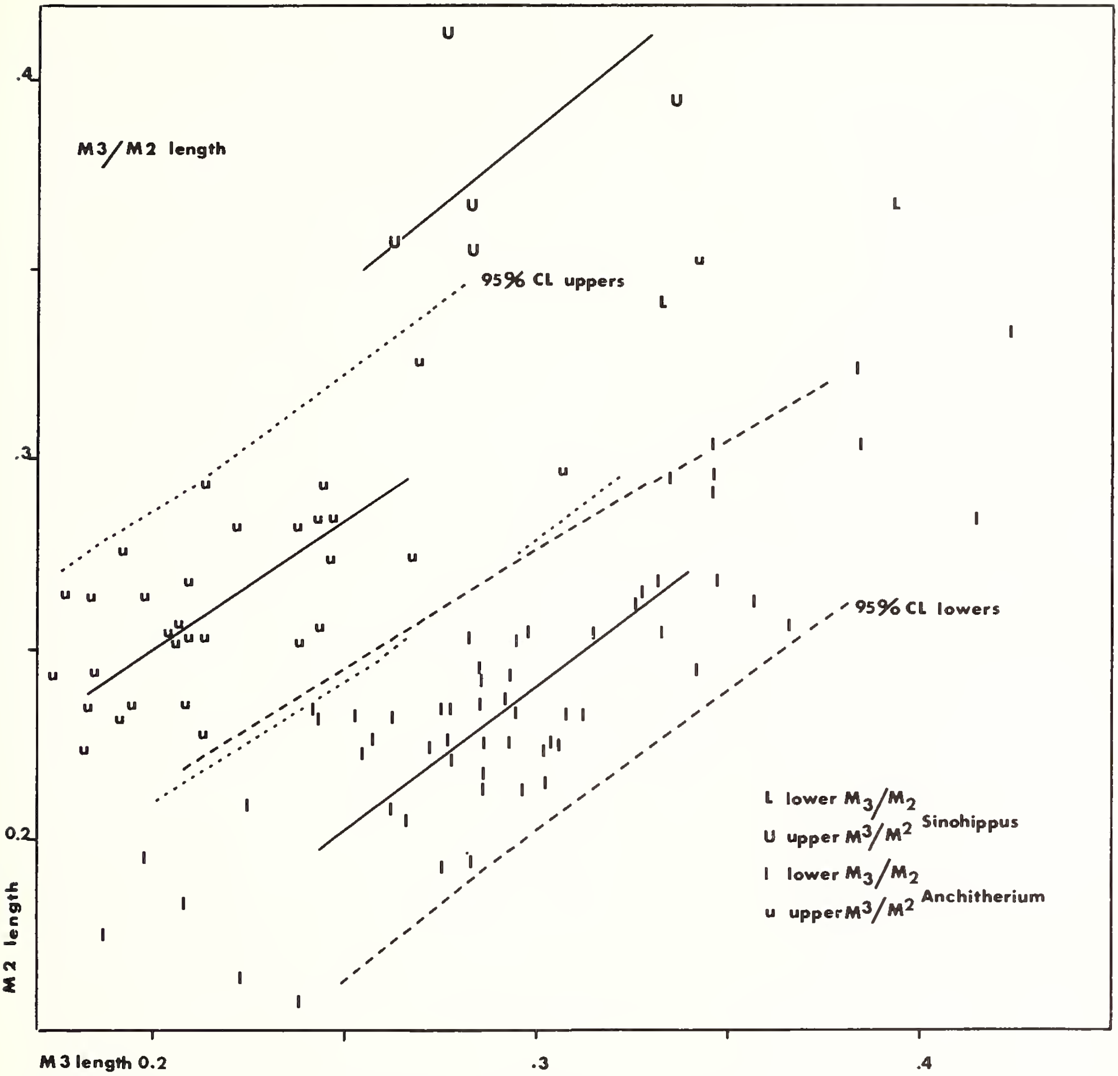


TEXT-FIG. 1. P3 length plotted against P2 length in Old World anchitheriines. Reduced major axis fitted to lowers and uppers of *Anchitherium*, and to uppers of *Sinohippus*. Ninety-five per cent confidence limits (95 % CL) drawn for the samples of *Anchitherium*. Log data.

Limb bones

Limb bones referable with certainty to *S. zitteli* are not known, but from the Meotian-Lower Pontian of Altan Teeli, Mongolia, there is a partial hind foot (PIN, numberless) comprising left MT III, II, and IV, phalanx 1^{III}, 1^{II}, and 1^{IV}, of a large anchitheriine, possibly *S. zitteli*. Anchitheriine teeth have not been found at Altan Teeli, but *Sinohippus* did occur in Mongolia: Schlosser (1924, p. 68; Taf. V. 10) referred a lower tooth fragment from Olan Chorea to *Hypohippus zitteli*, and from the Upper Miocene-Lower Pliocene of Hua Te, Inner Mongolia, there is a skull fragment with left P^{2-4} (PIN 2203-5) of this species.

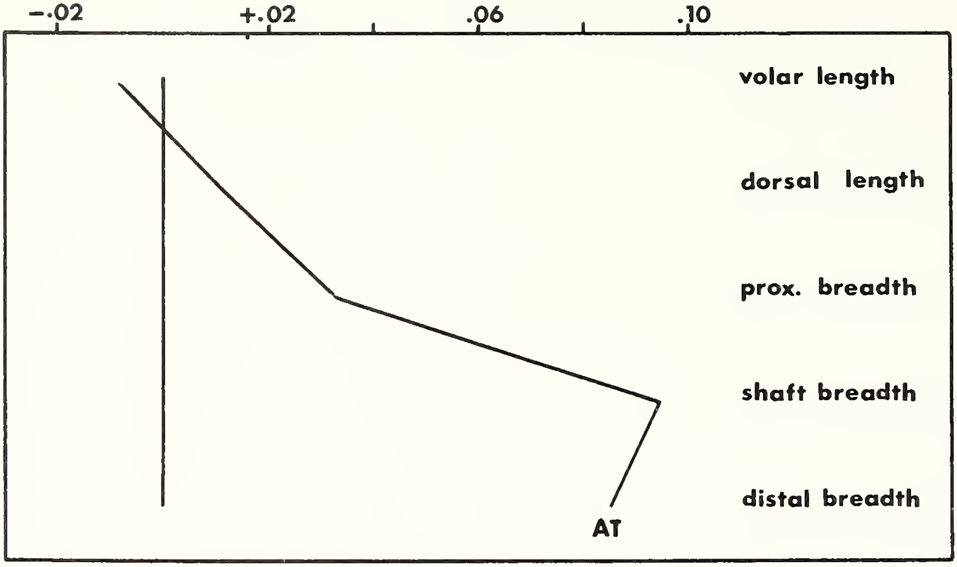
The metapodial from Altan Teeli is short, very robust, and anteroposteriorly flattened. The side toes are also very robust, the whole podial rather resembles that of a rhino. Phalanx 1^{III} is typically anchitheriine, however, with concave proximal volar scars for the attachment of the cruciate ligaments, and a broad, rugose scar for the central sesamoidean ligament. Compared with *Hypohippus* of similar size from the Lower Clarendonian of Cherry County, Nebraska (AMNH material), the podial and phalanx of *Sinohippus* are considerably more robust (text-figs. 3-4). MT III of large European forms of Upper Helvetian-Vindobonian *Anchitherium* (e.g. from Sansan, Steinheim, and La Grieve) are also more slender than those of *Sinohippus*. A scattergram (text-fig. 5) with phalanx 1^{III} mid-shaft breadth plotted against dorsal length, shows that Old World anchitheriines in general were more massive than the New World forms.



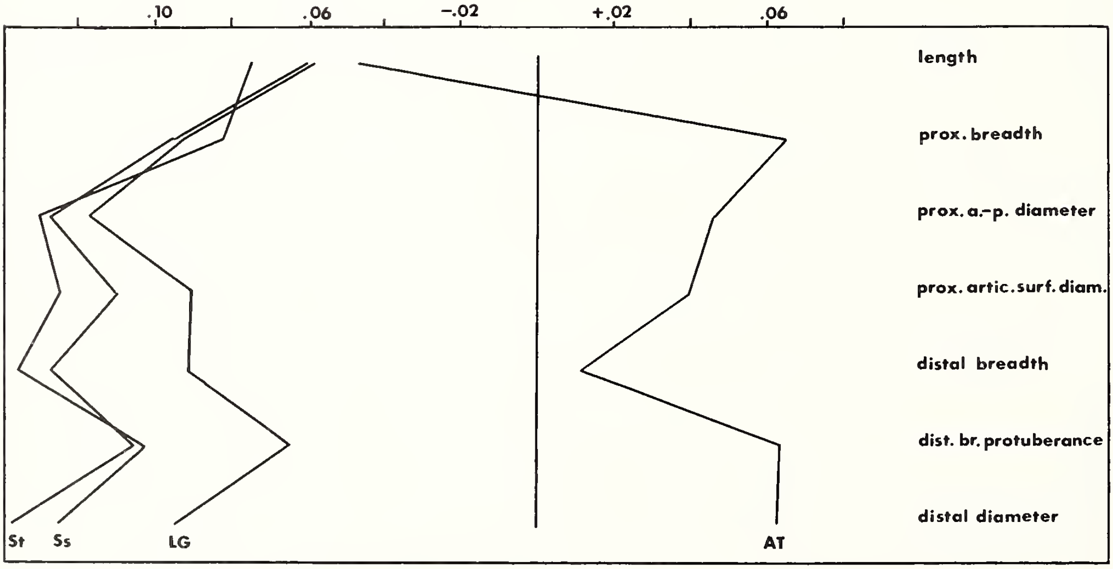
TEXT-FIG. 2. M2 length plotted to M3 length in Old World anchitheriines. Reduced major axes fitted to lowers and uppers of *Anchitherium*, and to uppers of *Sinohippus*. Ninety-five per cent confidence limits (95 % CL) drawn for the samples of Anchitherium. Log data.

DISCUSSION

The wide, ill-defined preorbital fossa and robust proximal phalanx place *Sinohippus* among the Old World anchitheriines. *Sinohippus* may have evolved from *Anchitherium* as Sondaar (1971, pp. 250–251) suggested. The scarcity of Upper Miocene anchitheriines in Eurasia is not positive evidence for evolution *in situ*; the possibility of repeated immigration of anchitheriine horses from the New World in the Middle and Upper Miocene cannot be excluded. The monotypic genus *Paranchitherium* Borissiak, with the single species *Karpinskii*, has been found in the Upper Helvetian–Vindobonian fauna of Belometžetskaya, Georgian S.S.R. (Borissiak 1938, 1945; Gabunia 1973), but nowhere else. *Paranchitherium* is much closer to New World *Parahippus* Leidy



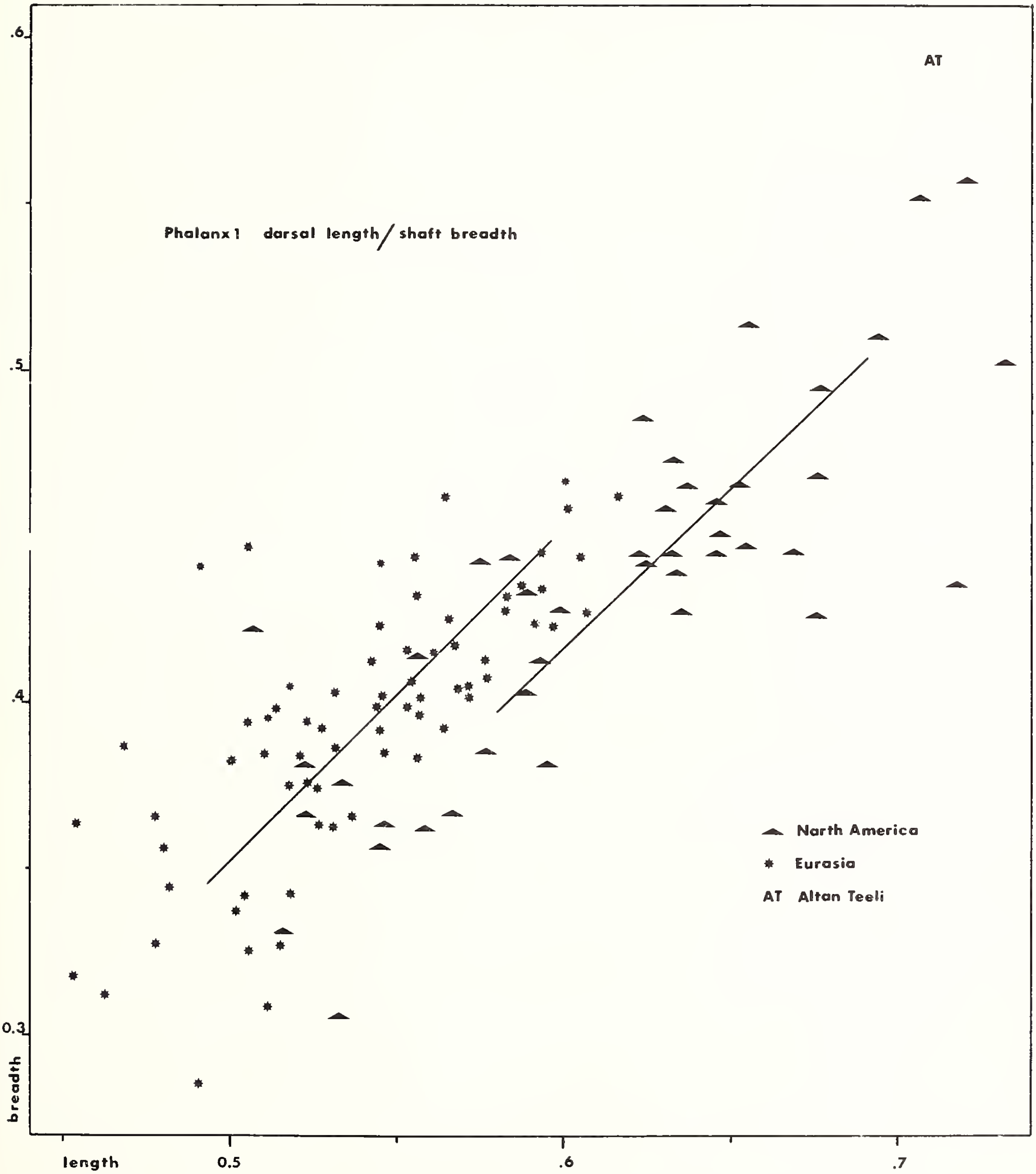
TEXT-FIG. 3. Ratiodiagram (Simpson 1941) comparing phalanx 1 of *Sinohippus* from Altan Teeli (AT) with *Hypohippus* (standard) from the Lower Clarendonian, Cherry County, Nebraska.



TEXT-FIG. 4. Ratiodiagram (Simpson 1941) comparing MT III of *Sinohippus* from Altan Teeli (AT), *Anchitherium* from Steinheim (St), Sansan (Ss), and La Grieve (LG) with *Hypohippus* (standard) from the Lower Clarendonian of Cherry County, Nebraska.

(e.g. *P. nebrascensis* Peterson), than to *Anchitherium*, in having a connected crochet, thin cement, and rather well-developed metaconid and metastylid (Borissiak 1938, 1945). It may represent an episodic immigration from the New World.

Sinohippus paralleled *Hypohippus* in reduction of P2/2 and M3/3 and in pronounced shearing crests of the teeth. *Hypohippus* occurred in the Barstovian and Clarendonian, replacing *Anchitherium*



TEXT-FIG. 5. Phalanx 1 mid-shaft breadth plotted against dorsal length in Eurasian and North American *Anchitherium* and *Hypohippus*. Reduced major axis fitted to the data. AT = *Sinohippus* from Altan Teeli. Log data.

over most of its range in North America. So far *Hypohippus* has not been found in the Upper Miocene fauna of Eurasia. Although in *Sinohippus* the reduced peripheral teeth and shearing crests were derived characters resembling *Hypohippus*, I believe *Hypohippus* and *Sinohippus* evolved in parallel. Both *Sinohippus* and *Hypohippus* (as well as some stratigraphically late *Anchitherium*) have been found occasionally in association with hypsodont-selenodont horses. They may have filled similar niches in the Upper Miocene fauna of their respective continents.

Sinohippus zitteli represents one of the stratigraphically youngest of the Anchitheriinae. According to Žegallo (1978, pp. 13, 21) the age of Altan Teeli and Hua Te, Mongolia, as well as Loc. 31, Shansi, is Upper Meotian–?Lower Pontian, i.e. Turolian–?Lower Ruscinian.

The stratigraphically youngest forms of *Anchitherium* occurred together with *Hipparion* in Upper Miocene faunas at: Nombrevilla, Spain (Villalta and Crusafont 1945); Soblay, France (Sondaar 1971); the Rhine Valley, Germany (v. Koenigswald 1929, 1931); Gaiselberg (Thenius 1950), Holzmannsdorfberg (Mottl 1970, p. 140), Brunn bei Nestelbach and Lassnitzhöhe bei Graz (Mottl 1954, pp. 64–65; 1955, pp. 51–58), Strass bei Lohnsburg (Thenius 1952), and Prottes (Zapfe, pers. comm.), all Austria; at Uşak (Ozansoy 1969) and Esme-Akçaköi (Sondaar, pers. comm.), Turkey; at Mogila Bortkutbai and Kalkaman, Kazakh S.S.R. (Tleuberdina, pers. comm.). Most occurrences are Vallesian/Middle Sarmatian; Prottes is Pontian in the Vienna Basin sequence (Zapfe, pers. comm.). *Sinohippus zitteli* may thus be even younger than the youngest forms of Eurasian *Anchitherium*. *Sinohippus* became extinct without leaving any descendants.

It is not known whether *Sinohippus* occurred elsewhere than in East and Central Asia. In *Anchitherium sampelayoi* Villalta and Crusafont from the Vallesian of Nombrevilla (Villalta and Crusafont 1945) P_2 does not appear to be reduced relative to P_3 (text-fig. 1, in squares). The reduction of M_3, maintained by Villalta and Crusafont (1945, p. 76), is uncertain. The single M_3 preserved cannot be measured since it is still lodged in the jaw. Even larger than *Sinohippus*, *A. sampelayoi* approached in size the gigantic, New World, *Megahippus matthewi* (Barbour). If the astragalus from Soblay and proximal MT III from Esme-Akçaköi, identified as anchitheriine (Sondaar 1971 and pers. comm.), indeed belong to this group of horses, they would presumably correspond to teeth the size of those of *A. sampelayoi*.

Zhai (1962, p. 55) believed the Vallesian *Anchitherium* from the Rhine Valley to be more closely related to *Sinohippus* than to *Anchitherium aurelianense* (Cuvier), but this cannot be ascertained because peripheral tooth pairs are lacking from the Rhine Valley. The Rhine Valley teeth resemble those of the similarly large *Anchitherium* from the Upper Helvetian–Vindobonian of Sansan and La Grieve.

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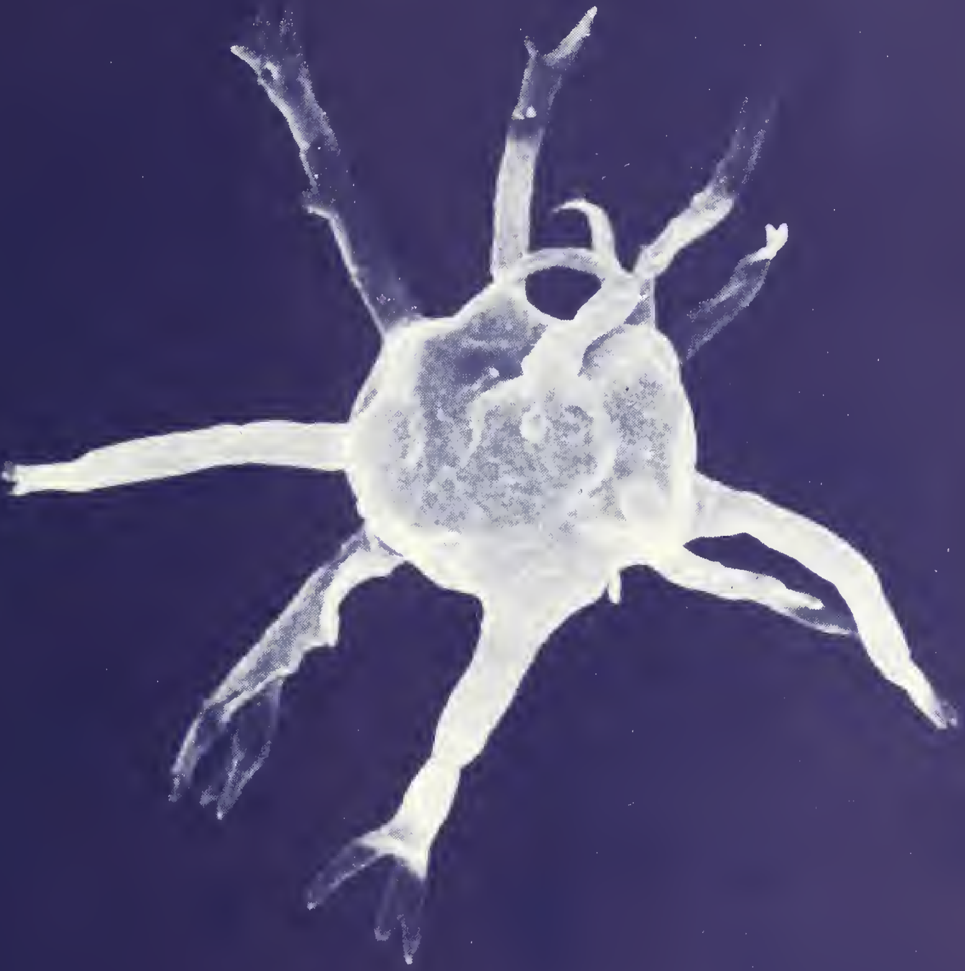

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Cover: An acritarch of the genus *Multiplicisphaeridium* from the Tournaisian Bedford Shale of Ohio, U.S.A. Institute of Geological Sciences specimen number MPK 3569. S.E.M. × 1000. Within the last twenty-five years the number of described acritarch taxa has increased dramatically, and these organisms are now used extensively to date rocks of late Precambrian to Devonian age.

FOSSIL FORESTS FROM THE LOWER CRETACEOUS OF ALEXANDER ISLAND, ANTARCTICA

by TIMOTHY H. JEFFERSON

ABSTRACT. Fossil forests and forest floors have been found in the Lower Cretaceous part of the Fossil Bluff Formation in south-east Alexander Island, Antarctica. These grew at an apparent palaeolatitude of 65° to 75° S., within the Cretaceous polar circle. Analyses of the well-preserved growth patterns have yielded important information about periodicity of growth, and the effect of rapid burial on trees. Increments of annual growth were very variable and growth rates were high. These growth characteristics are very different from those of modern high-latitude trees. They compare most closely with some species of living trees growing in warm temperate areas with a long growing season. The palaeoclimatic information is apparently inconsistent with the high palaeolatitudes proposed in most existing palaeocontinental reconstructions.

THE Upper Jurassic–Lower Cretaceous Fossil Bluff Formation crops out as a coastal strip of well-exposed cliffs and nunataks on the east side of Alexander Island, Antarctica (text-fig. 1*a*, *b*). Fluviatile and lacustrine sedimentary rocks occur in the southern part of this formation and are of Aptian–Albian age (Taylor, Thomson, and Willey 1979). Within this part of the succession occur abundant fossil leaf floras (Jefferson 1981 and in prep.) and several fossil coniferous forests. The sediments which now constitute the rocks of the Fossil Bluff Formation accumulated in a fore-arc basin (Suárez 1976). Most of it was derived from a volcanic-arc source 20–40 km to the east and has a high volcaniclastic component. The silicification of the secondary wood of conifers within the fossil forest can be attributed to early diagenesis of these sediments, decomposition of volcanic material, and release of free silica. The processes of decay and mineralization of the fossil wood, together with the taxonomy, are discussed in detail in Jefferson (1981), and will be the subject of a forthcoming paper.

PALAEOGEOGRAPHY

Reconstructions of Early Cretaceous palaeogeography position south-eastern Alexander Island within the Cretaceous polar circle. The most recent reconstruction with the largest data base is that of Smith, Hurley, and Briden (1981), in which south-east Alexander Island is at 74° S. Lesser Antarctica, however, is now considered to be made up of at least three plates, the Antarctic Peninsula, Ellsworth, and Thurston plates (Baker and Griffiths 1977; DeWit 1977). Text-fig. 2 is a combination of a 110 ma reconstruction produced by Dr. A. Smith (computer program as in Smith *et al.* 1981) with the possible range of positions of the Antarctic Peninsula plate. Palaeolatitude varies from 69° to 75° S. A limited amount of palaeomagnetic data from the Antarctic Peninsula gives a 110 ma palaeolatitude of 65° S, but this involves an error margin of ± 10 degrees (Kellogg 1980). The palaeomagnetic control for the stable continental blocks of South America and East Antarctica is much better. The range of positions of the Antarctic Peninsula relative to these is limited by the structural continuity of the southern Andes and the Antarctandes and by geological and palaeomagnetic evidence. This evidence fixes the northern end of the Antarctic Peninsula close, or adjacent, to the southern tip of South America (Dalziel and Elliott 1973; Barker and Burrell 1977). Reconstructions involving a wide separation between the Antarctic Peninsula and South America

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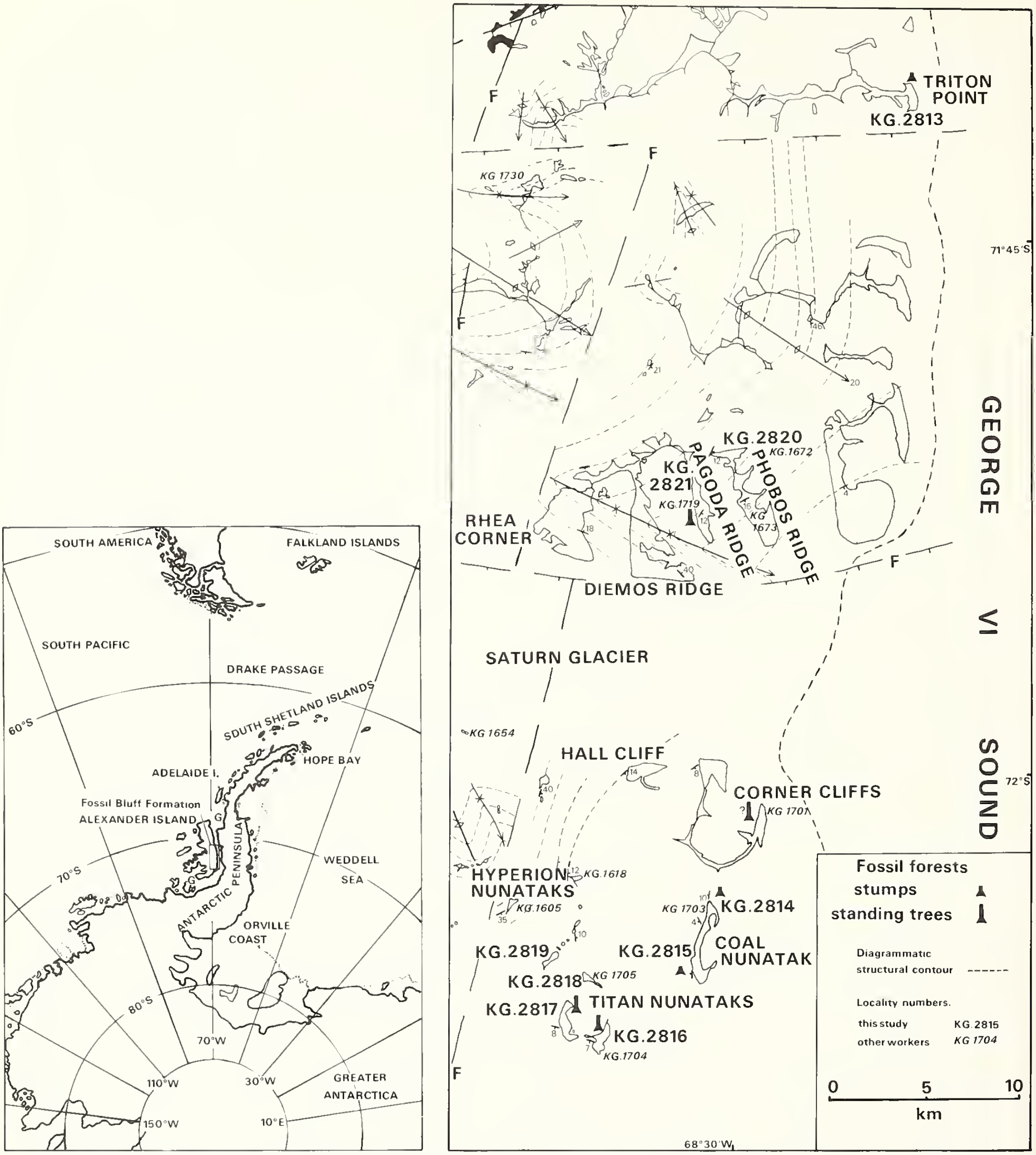
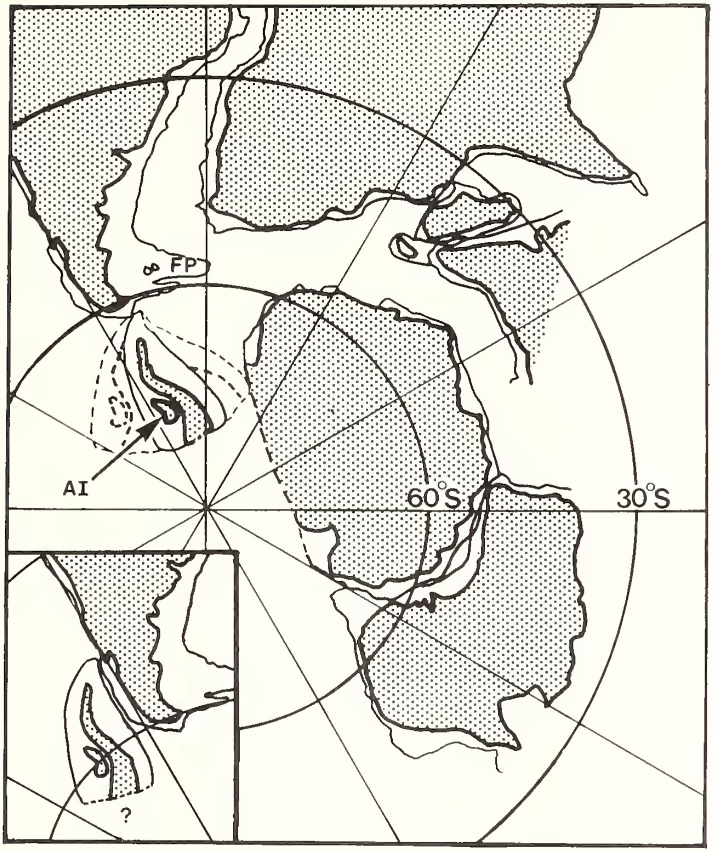


TEXT-FIG. 1. (*a*) Map of Lesser Antarctica showing localities used in text. Position of text-fig. 1*b* indicated. (*b*) Map of south-eastern Alexander Island showing positions of fossil forest floors and standing-tree fossil forests.



TEXT-FIG. 2. 110 ma reconstruction of the southern continents showing possible positions of the Antarctic Peninsula plate. Computer map by A. G. Smith (using program as in Smith *et al.* 1981). Shape of Antarctic Peninsula plate after Dewit (1977). Inset shows a possible position of the Antarctic Peninsula plate adjacent to southern South America (see text).

during the Early Cretaceous are, therefore, unlikely. Reconstructions using the expanding earth model (Owen 1976) also reposition south-east Alexander Island within the Cretaceous polar circle at a latitude of 67° S.

WOOD TAXONOMY

The taxonomy of the fossil wood presented considerable problems and a full discussion is beyond the scope of this paper. However, some of the problems involved are summarized below:

1. The classification of fossil wood is at present unresolved. Comprehensive keys (e.g. Krausel 1949) are effective only when crucial details of fine structure are preserved. Some diagnostic structures have been obscured or modified by decay and mineralization in the Alexander Island fossil woods.
2. Structural variability of wood from different parts of individual trees leads to complications in classification of fossil material which require more careful consideration than has usually been given.

3. Although the Alexander Island fossil woods are clearly gymnospermous, composed mainly of tracheids (vertical elements) and medullary rays (radial elements) and are devoid of resin ducts, they show characteristics of tracheid and ray pitting which are intermediate between the 'Araucaria type' and 'Cupressus type' groupings. Therefore the two taxa which were recognized cannot be referred satisfactorily to any existing genera or species.

The two taxa are distinguished on the presence or absence of parenchyma cells, the parenchymous wood bearing distinct, ?resin-filled parenchyma cells distinct from and smaller than the surrounding tracheids. These cells occur throughout the growth ring. Both woods are characterized by well-marked growth rings of variable size; transition from early- to late-wood cells is gradual over the ring but abrupt in the last 5–7 cells terminating in 3–5 small thick-walled cells. Bordered pits are borne only on the radial walls of tracheids and are predominantly circular, uniseriate, and separate. Medullary rays are uniseriate, variable in height (1–33 cells), and are composed of cells which are rectangular in tangential section but which may be round or oval. The ray cells are pitted only on tangential walls (walls adjacent to tracheid walls) and the cross-field bears one oval or two round pits.

In terms of the cross-field pitting both woods agree most closely with the genus *Circoporoxylon* Krausel but some species within *Phylocladoxylon* Gothan and *Protocupressinoxylon* Eckhold are equally comparable. Some proposed solutions to the problems encountered in the classification of the fossil woods, together with a full systematic description of them, will be presented in a forthcoming paper.

PREVIOUS RESEARCH ON FOSSIL FORESTS

Although much has been written about fossil wood and isolated standing trees (see Chaloner and Creber 1973, and references therein), far less is known about fossil forests. There are a number of accounts of Carboniferous standing tree fossil forests, but very few of these contain any truly petrified trees. The *Sigillaria* trunks of Joggins, Nova Scotia, studied mainly for the vertebrate fauna which the hollow trunks contain (Carroll *et al.* 1972), the lycopods of the Francis Creek Shale, Illinois (Shabica 1979), and the *Lepidodendron* trunks of Victoria Park, Glasgow (Seward 1919) all decayed and were subsequently filled by sediment. One exception is the calcified forest floor on the north coast of the Isle of Arran (Tyrrell 1928), but most of the stumps have now either been removed or eroded by the sea and provide little opportunity for further study. Krasilov (1975, p. 34) mentioned six horizons of forest development in the Middle Jurassic of the Yagnob river valley (Siberia), where burial was by mud-flows. He also described a Cretaceous conifer forest in the Ana Darya area of northern USSR, where trees are coated in ferruginous sheaths. Calcified fossil conifer stumps make up the Cretaceous 'Purbeck Forest' of the Great Dirt Bed of Dorset and are preserved in supratidal algal burrs (Jane Francis, pers. comm.). Francis found that growth rings were highly variable (though less so than in the Alexander Island fossil woods) and attributed this to an arid climate.

Calder (1953) described a Tertiary *Araucaria*-dominated forest preserved in rhyolitic ash in the Desearo river valley, Patagonia. As this is highly silicified, and little organic material remains, few growth rings are preserved. This forest, like the other Tertiary Argentinian forests and the famous petrified forest of Arizona (Ash 1970), is made up almost entirely of fallen trees. The silicified forest near Sarmiento, northern Patagonia, consists of fallen *Araucaria* logs in red sandstones and siltstones (pers. obs. 1979). Preservation of rings and cell structure is excellent, with fine details like the tori (the membranes in the centre of bordered pits) preserved in silica. The best documented fossil forests are those of Yellowstone National Park, north-west USA. Although these are all Tertiary in age (Dorf 1964), the sedimentary and diagenetic environments leading to mineralization appear to be similar to those in Alexander Island. Dorf (1964) regarded many of the Yellowstone Park forest beds as volcanic debris flows, but recent work by Fritz (1980*a*) suggests that most of the trees were buried by alluvial sandstones and conglomerates. These are 80–90% water-transported air-fall ash and 10–20% reworked detrital volcaniclastic material. The preservation of growth rings and cell structure in Yellowstone Park is comparable with, but rather more consistent than, the Alexander Island material, probably because of the higher percentage of volcanic material in the sediment (see Jefferson 1981).

THE ALEXANDER ISLAND FOSSIL FORESTS

Distribution

Most of the fossil wood found in the Fossil Bluff Formation occurred in the form of standing trees and stumps and the term 'fossil forest' is used in this study for any group of trees or stumps which are clearly in position of growth at a distinct stratigraphical level. The number of trees constituting a fossil forest depends on the area of its exposure, rather than on the original area of tree cover; whenever a bed contained *in situ* stumps at one outcrop, stumps were also found in all nearby but separate exposures, suggesting continuous tree cover over areas of at least 1 km^2. *In situ* fossil forests were found at seven of the localities shown in text-fig. 1*b* (KG.2812, KG.2813-16, KG.2820, and KG.2821) and it is mainly with these that this paper is concerned.

Some of the fossil wood, however, occurred as isolated branches and trunks which were transported from the site of growth and deposited at a low angle to bedding within fluvial sandstones. Transport and break-up of the trunks and branches probably took place during flooding. Trunks transported by mud-flows and deposited in an upright position as described by Fritz (1980*b*) were not seen. Drifted wood was often found in sandstone units at the same stratigraphical level as fossil forests and most of this material was probably derived locally from these forests. At other stratigraphical levels, however, some of the wood is likely to have been derived from more varied or more distant sources and represent true 'drifted assemblages'. The recognition of these on the basis of growth patterns is discussed below.

Modes of preservation

The form of each fossil forest is determined by the type and extent of mineralization, and this, in turn, is related to the way in which the trees were buried. The processes of decay and mineralization are discussed in detail in Jefferson (1981). The characteristics of the sediment which control silicification are 1, grain size; 2, mineralogy; and 3, porosity. Substantial quantities of mineral-rich fluid (in this case the mineral is free silica) must be available before decay takes place, and this fluid must be highly mobile within the sediment. Secondary wood buried in sediment with a low primary porosity is not permineralized because of low availability and mobility of free silica, but decomposes and becomes carbonized as sediment compaction takes place. Thin coalified lenses and sheets of coaly material, commonly found within the finer-grained rocks, are the only remnants of trunks and branches. Burial by sediment with a low volcaniclastic component also led to preservation failure, irrespective of porosity, because early generation of free silica depends on the diagenetic breakdown of metastable volcanic material (Sigleo 1979). Coarse volcaniclastic sediment with a high porosity provides the optimum conditions for petrifaction. Point-counting of thin sections of sandstones from the east Titan Nunatak fossil forest indicates that 70–85% is detrital volcaniclastic material. Trees may be buried in this type of sediment in two ways:

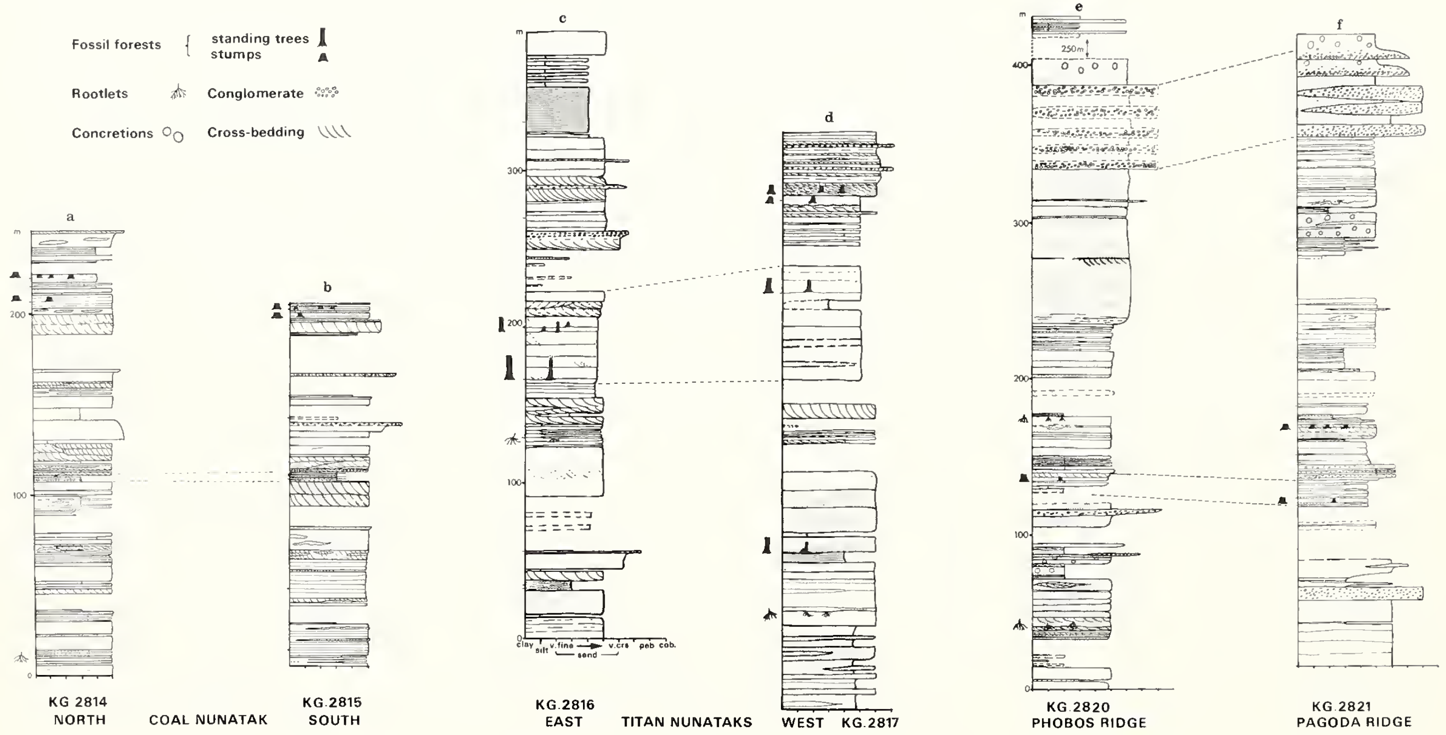
1. By a single influx of sediment: because the coarse volcaniclastic sandstone units are usually only 25 cm thick and rarely more than 1 m thick, only the stumps and basal portions of the trunk are enclosed in sediment favourable for mineralization (Pl. 66, figs. 1–2). Where burial of the rest of the tree was by fine non-volcaniclastic sediment, the upper trunk was not preserved. Forests buried in this manner are preserved as fossil forest floors (best seen at the top of nunataks where large expanses of near horizontal bedding planes are exposed). Forest floors are also exposed in cliff sections, but it is likely that many were not recognized in the field due to indifferent preservation, lateral discontinuity of tree cover, and/or the possibility that a short cliff section through a forest floor might not intersect a tree.
2. By repeated influxes of sediment: provided that the intervals between these influxes were not sufficient for death and decay of the trees to occur, trunks were preserved as standing trees. Standing-tree fossil forests are exposed only in cliff sections, where trees up to 6 m high are found (Pl. 66, figs. 3–5).

There are gradations between those sediments most favourable for mineralization and those in which mineralization is impossible. Wood preserved in medium-grained sandstones with a low to moderate volcanic component is highly carbonized and sparsely distributed. Partial mineralization of trees is common, and no tree has been completely or uniformly preserved.

GENERAL FEATURES OF THE FOSSIL FORESTS

Forest floors

Petrified tree stumps were found at all seven localities which are studied in detail. In several cases these were poorly preserved and apparently isolated (either because of preservation failure or as a function of the original distribution). Stumps can be recognized as the remains of trees within a



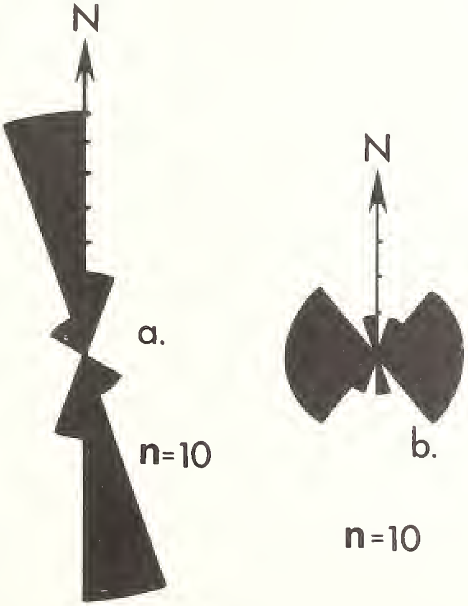
TEXT-FIG. 3. Stratigraphic logs of localities studied in detail. Lithological correlation by eye.

forest rather than of isolated trees in four cases. The location of these is shown in text-fig. 1*b* and the stratigraphical position in text-fig. 3. The two most extensive floors will be described in more detail.

At Triton Point (KG.2813) fossil forest floors are exposed at two levels, 5 m apart, at the top of the cliffs. There are two exposures of the upper forest floor horizon, one with eight exposed stumps and one with six, and one of the lower with six stumps. Although the relationship between the two is not clear, they are regarded as a single forest and it is likely that the first forest survived, at least in part, and gave rise to the second. The stumps are preserved in a medium-grained white tuffaceous sandstone which is devoid of sedimentary structures. Roots which penetrated the underlying coarse brown sandstone, decayed, were filled by sediment during compaction and are now preserved only as casts with a carbonized coating. The original soil has been compacted to an irregular carbonaceous palaeosol less than 2 cm thick. The margins of all stumps are carbonized and poorly defined due to pre-petrifaction decay.

At the South Coal Nunatak (KG.2815) an extensive fossil forest floor is exposed on a single bedding plane at the summit of this flat-topped nunatak. The floor occurs 1·45 m from the top of the section (text-fig. 3*b*) with a total exposure of 25 × 38 m and a total of fifty-four *in situ* stumps: thirty-one of these occur in an unbroken exposure 22 × 25 m. Stumps vary in diameter from 22 to 8 cm and have weathered out from a coarse brown sandstone with a high volcanic content (Pl. 66, figs. 1–2). The stumps are between 3 and 5 m apart, with an average density of 1 per 17 m^2 and an average spacing of 4·2 m. Where a thin layer of the overlying fine white tuffaceous sandstone covers the forest floor, parts of the trunks are totally carbonized.

Many of the stumps are asymmetrical with a consistent north–south trend (text-fig. 4*a*). Jointing, and subsequent frost shattering and weathering, however, are thought to have produced these shapes. Close examination of the growth rings indicates that the original cross-sectional shape of the trees was very different from the stump shapes produced by these secondary effects. The marked asymmetry of growth rings in many stumps has a wide range of orientations (text-fig. 4*b*). These are as likely to have been produced by local effects of competition (shading, etc.), as they are to have been a product of preferential growth towards low incident light (Kossovich 1935; Smirnoff and Connelly 1980), strong prevailing winds (Schwarzbach 1963), or angle of slope (Dorf 1933).



TEXT-FIG. 4. (*a*) Rose diagram of long axes of asymmetrical fossil stumps measured in the field (Triton Point and Coal Nunatak south). (*b*) Rose diagram of long axes of asymmetrical growth-rings from oriented samples of stumps from the same localities.

Standing tree fossil forests

Standing tree forests were found at three distinct stratigraphic levels at four localities (KG.2815, 16, 17, and 21; see text-figs. 1*b* and 3), and in varying states of preservation. At least one other has been reported from Corner Cliffs (Pl. 66, fig. 3) (L. E. Willey, unpublished field notes), a locality not studied in the course of this work. A few isolated standing trees also occur in poorly exposed or inaccessible beds.

The trees in two of the forests were preserved to a height of only 1 m and much of the wood collected was found to be poorly preserved. The fossil forest exposed in a cliff 1·5 km long at east Titan Nunatak is, however, well exposed and is also seen at west Titan Nunatak. At east Titan Nunatak the standing trees are preserved in a coarse volcaniclastic sandstone unit 17·3 m thick. Text-fig. 5 shows the detailed stratigraphy of this unit, in which at least four of the bedding surfaces exposed in cross-section were forest covered. The flask-like shape of the basal portion of several of the trees suggests that they survived the influx of sediment (Pl. 66, fig. 4). This shape is common in modern conifers when roots and basal parts of trunks have been covered for long periods by standing water or sediment. Stone and Vasey (1968) found this form of retardation in radial growth of redwoods from western Canada. This was because of reduced root aeration when they were inundated by flood water and buried by silt up to 120 cm thick. The trees also developed new roots in the top layers of the newly deposited sediments. Krasilov (1975), who described this type of broad tree base as 'hygrophytic', also noted the development of adventitious roots, but there is no evidence of the latter in any Alexander Island fossil trees. Land surfaces formed by newly deposited sediment were apparently rapidly colonized by trees. These often grew within 1 m of other trees which had probably survived inundation (Pl. 66, fig. 5).

The suggestion that at least some of the trees survived sediment influx is supported by the fact that most of their height is above the surface formed by the first sediment influx. The height of the tallest tree remains found is 7 m, and of this at least 5 m protrudes above the first bedding plane. However, modern trees killed by the influx of sediment, or by standing water, sometimes withstand decay for several decades. For example, trees at the margins of Lago Argentino (Argentina) are periodically submerged (pers. obs. 1979). The Perito Moreno glacier forms an ice dam at five- to twenty-year intervals, and the water level rises until the dam collapses. Although all the trees are killed by the submergence, many remain in an upright position for many years. In this case water-logged fallen trees are common below the water line.

Fallen trees and branches are rare in Alexander Island fossil forests, suggesting that loose woody material drifted off and was carried away before it became waterlogged. In the Yellowstone Park fossil forests more than 60% of trees are in a horizontal position (Fritz 1980*a*, *b*). Transported trees commonly became wedged against standing trees when flooding of the Potomac river in 1961 buried

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EXPLANATION OF PLATE 66

Fig. 1. Silicified stump in the fossil forest floor at Coal Nunatak south. Specimen KG.2815.254 taken from upper left to stump.

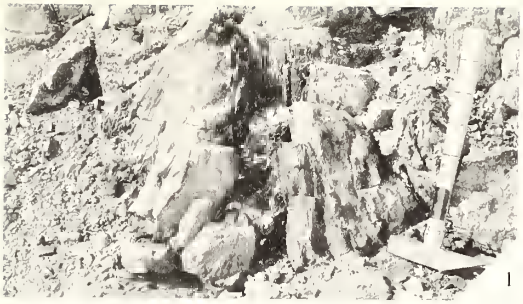
Fig. 2. Silicified stump in cliff section at same level as fig. 1.

Fig. 3. Silicified standing tree 3·05 m high from corner cliffs. Note curved form of trunk. Photograph by L. E. Willey.

Fig. 4. Silicified standing tree at east Titan Nunatak (see text-fig. 5). Trunk shown is 1·65 m high but continues for a further 1·05 m. Note impressions of roots and bulbous base. Specimen KG.2816.39 taken from 1 m height on left side of outer trunk.

Fig. 5. Three trees (*a*, *b*, *c*) in standing-tree fossil forest as in fig. 4. Tree on left (*a*) has fallen from cliff leaving silicified material only at base. Central tree (*b*) as in fig. 4.

Fig. 6. Carbonized rootlets in coarse tuffaceous sandstone 130 m from the base of section KG.2816 (see text-fig. 3*c*).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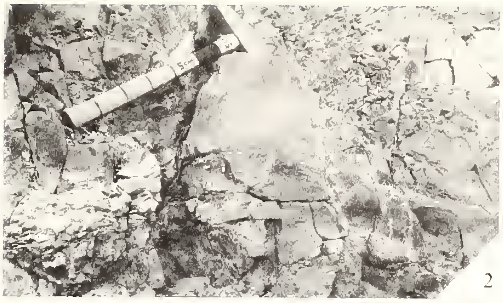
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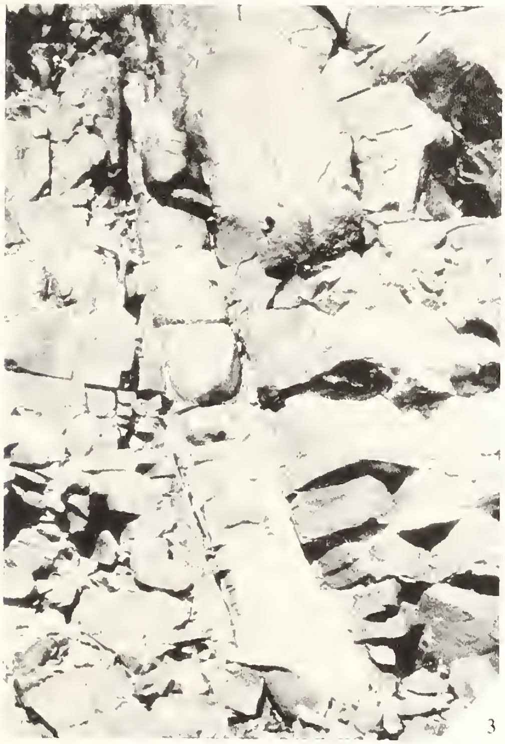
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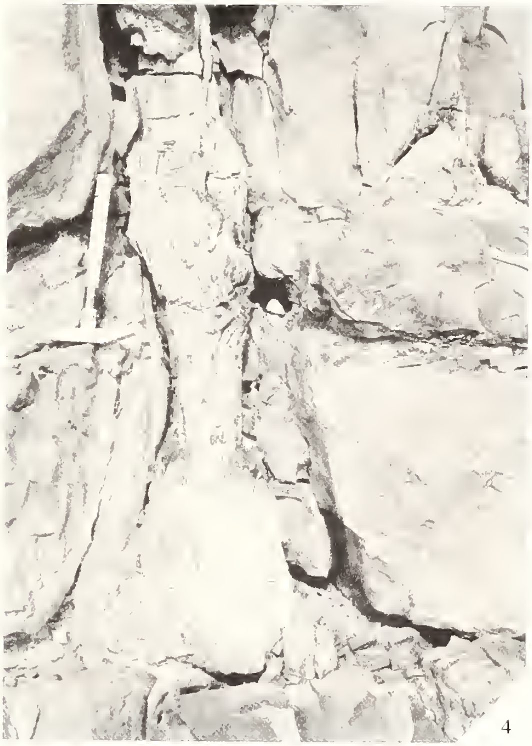
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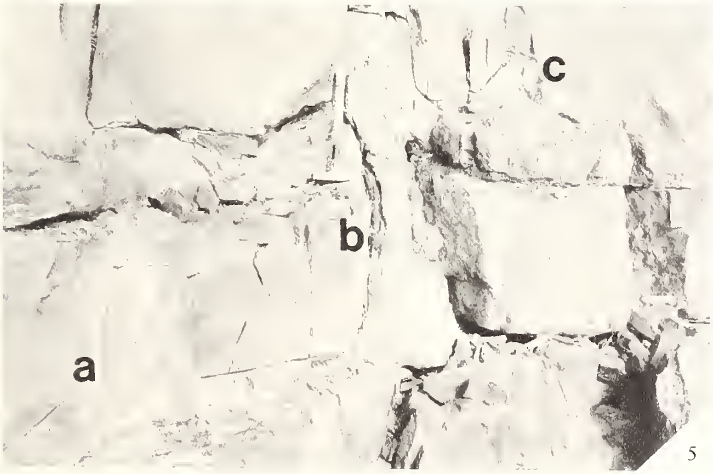

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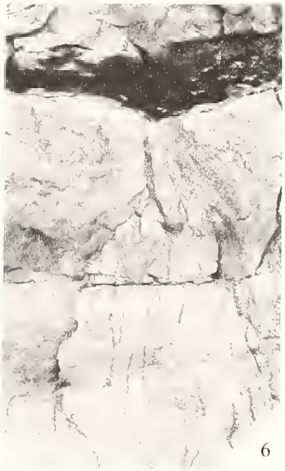
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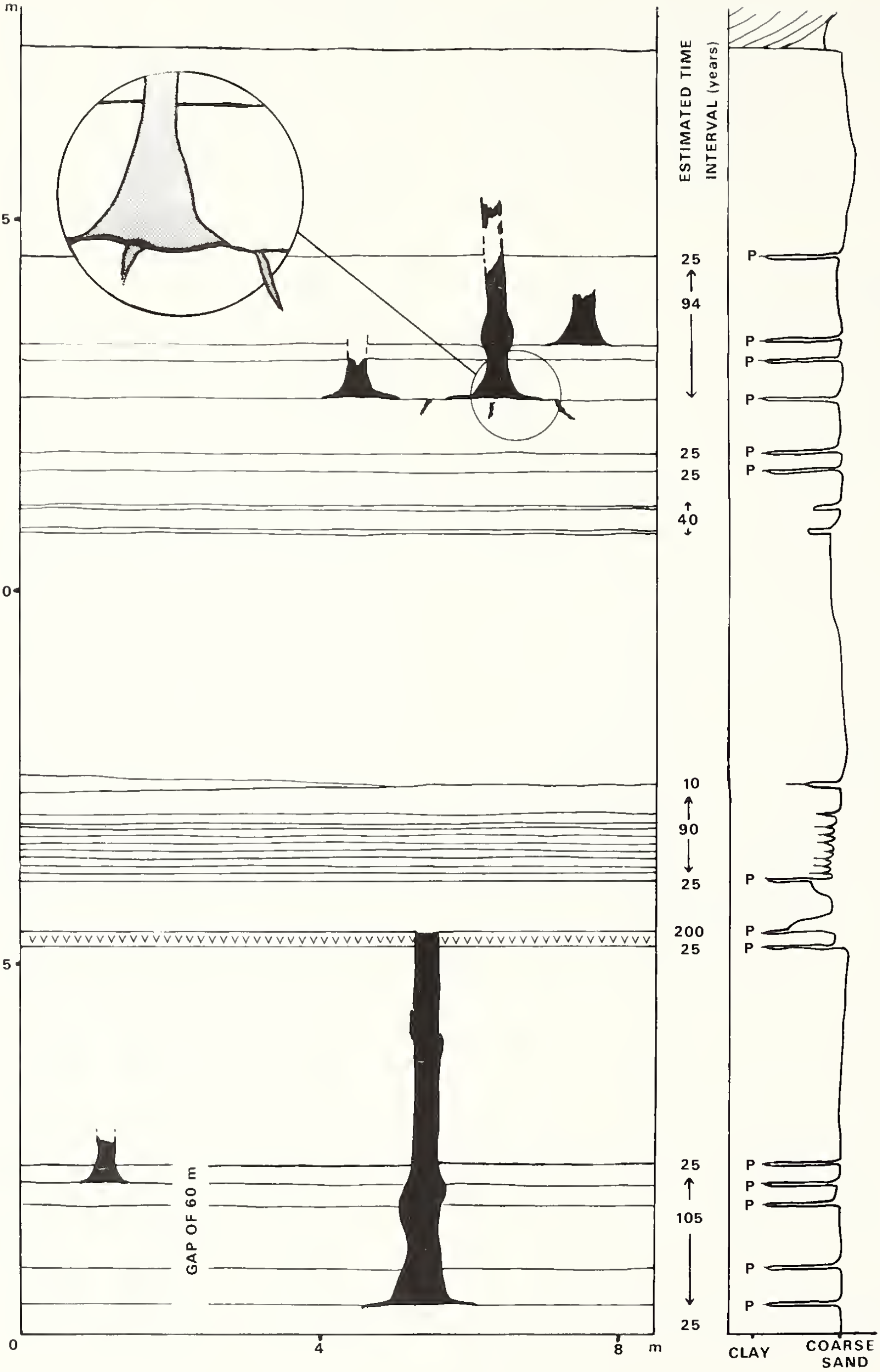
JEFFERSON, fossil forests



TEXT-FIG. 5. Detailed section through part of the unit containing the standing-tree fossil forest at east Titan Nunatak (see text-fig. 3*c*). vvvv = tuff bed. P = palaeosol.

several forested areas. The current velocities recorded during this flooding (Sigafoos 1964) were in excess of 20 ft/sec (6·1 m s^{-1}), which was sufficient to transport not only large fallen trees, but also several tons of concrete bridgework. Most mature trees survived the Potomac floods, but many young trees and saplings were killed by persistent standing water. The basal parts of trees were in some areas buried in 3 ft (0·9 m) of sediment, a thickness comparable with the beds of east Titan Nunatak. An absence of fallen trees in the Alexander Island fossil forests suggests that few trees were uprooted by flooding and that standing water, capable of floating fallen trees and branches free, was more persistent. The immature volcanic component is likely to have been weathered into clay minerals before colonization could take place but there are no well-developed palaeosol profiles. The forests developed in an immature soil, probably consisting of leaf litter and the layers rich in decomposed organic material. Lack of a well-developed podzolic soil profile may have been due to excessive waterlogging, or, more likely in view of the successful growth of conifers, to insufficient time between depositional events. Present-day mature soils may take over 5000 years to develop (Fitzpatrick 1971).

Roots were confined to this fine-grained, organic-rich soil and were therefore in a position of low preservation potential. They were also subject to compaction, which reduced soil thicknesses considerably. Calculation of original soil thickness was attempted using roots from east Titan Nunatak (Pl. 66, fig. 3, text-fig. 5). Casts of roots with a carbonaceous coating extend from the tree through the thin remnant palaeosol layer, and into the underlying sandstone. Extrapolating the position at which the roots would join the base of the trunk, were it raised to its pre-compactional position, gives an estimation of the amount of material lost by compaction. In this case an original soil approximately 35 cm deep is now represented by a layer 3·6 cm thick, a reduction of 90%. This depth of organic material is common in modern podzolic soil profiles (Fitzpatrick 1971). These residual palaeosols are packed with poorly preserved leaf litter, but no leaf material can be precisely identified. Rootlets, on a much smaller scale, are occasionally preserved within the coarse volcaniclastic beds. Although no cellular detail is preserved, the general pattern of rooting is clear (Pl. 66, fig. 6).

GROWTH RING MORPHOLOGY

Reaction-wood

Examination of the growth patterns reveals a rapidly developed asymmetry in some trees (Pl. 67, figs. 3–4). Growth rings which are very small or even absent on one side of the trunk are up to 5 mm across on the other. This is interpreted as reaction-wood and is found both in specimens from standing trees and from those not found in growth position, many of which probably represent branch material. This sort of growth pattern is typical in the trunks and branches of modern trees which have been tilted from the vertical. Ewart and Mason-Jones (1906) first pointed out that the formation of this asymmetric wood is a response to a gravitational stimulus. Sinnot (1952) recognized the development of 'reaction-wood' as a regulatory mechanism to restore or maintain the geometric relationships among parts of a tree and to maintain vertical growth in the trunk.

In the case of branches, which are permanently non-vertical, reaction-wood develops throughout the life of the tree as a regular asymmetry. Spurr and Hyvarinen (1954) reported that reaction-wood develops as a response to temporary bending of trunks, even if they revert to the vertical, as on the lee side of trunks after high winds, and explained the 'negative geotropism' as being instigated by increased concentrations of auxins on the underside of tilted branches and stems. Nečesaný (1958) suggested that the auxin responsible, for reaction-wood growth was β-indole-acetic acid. Robards (1969) confirmed that, in both angiosperms and gymnosperms, the response to a gravitational stimulus is triggered off by the 'redistribution of endogenous growth substances', and stated that 'reaction-wood allows aerial organs which are displaced from the vertical in woody plants to maintain or resume their predetermined growth positions'. Robards (1965) also stated that a tilt of only five degrees is capable of stimulating the production of reaction-wood. The response in angiosperms is to lay down tension-wood on the upper side of tilted stems, while the response in gymnosperms is to produce compression-wood on the underside. Angiosperm reaction-wood is not considered here. Published descriptions of reaction-wood in fossil trees appear to be confined to a single specimen of a late Jurassic gymnosperm from Norfolk, and to several specimens in the Carboniferous lycopod genus *Lepidodendron* (Creber 1972).

Marked reaction-wood development is common in the Alexander Island trees (Pl. 67, figs. 3–4). Of the thirty-three sufficiently large and well-preserved cross sections examined in detail, fourteen had at least one area of marked asymmetry developed during a single year's growth, and accentuated by further asymmetric growth over a period of 2–6 years (KG.1703.24; KG.1704.10, 11; KG.2813.1, 15; KG.2814.252–254, 256; KG.2815.71, 77; KG.2816.39; KG.2817.15, 16). The interpretation of all such asymmetries as responses to a gravitational stimulus, however, must be treated with some caution. Slash pine trees in Florida develop discontinuous growth rings when growing in high-density stands (Larson 1956). Suppression of the crown on one side of the tree through shading by other trees is thought to lead to reduced auxin production just below expanding buds. Delayed arrival or absence of these hormones on one side of the tree suppresses cambial activity and growth is reduced. Growth rings are often absent on one side of the tree or represented only by a few late wood cells. However, both Robards (1965) and Creber (1975) pointed out that the characteristics of cells of true reaction-wood in most trees are different to those of 'normal wood'. Many of the anatomical features, and all the chemical features such as the high concentration of lignin in cell walls, are unlikely to survive mineralization. In many of the asymmetric rings, preservation is not good enough to recognize any subtle morphological differences. Nevertheless, in several specimens, cells in the reaction-wood are markedly rounded and have thicker cell walls than their normal counterparts (Pl. 67, fig. 5). Intercellular spaces are also larger and more common. The much more gradual transition in cell size from early to late wood in reaction-wood (Carrara 1979) is also seen in these specimens. Unfortunately, the markedly helical striations on tracheid walls (Pl. 67, fig. 6), described as indicative of reaction-wood (Côté and Day 1965), are not distinguishable from those resulting from pre-mineralization decay, or splitting at the time of mineralization. It is probable that at least some of the rapidly developed asymmetries represent reaction-wood induced by a gravitational stimulus.

Reaction-wood production after tilting of trees by various natural causes is documented. Trees bent by avalanches produce reaction-wood on trunk and branch undersides (Burrows and Burrows 1976; Carrara 1979). In some cases, growth rates are abruptly increased, due to reduction in competition, whereas in others they decrease because of loss of foliage. The 1958 movement of the Fairweather fault, south-east Alaska, tilted many conifers (Page 1970) and reaction-wood developed the following year, the maintenance of the geometric relationships between trunk and branches being effected by particularly marked reaction-wood development in the branches. Movement of the San Andreas fault in California caused similar tilting of trees and production of reaction-wood (LaMarche and Wallace 1972). In Colorado, erosion of roots has been shown to cause slight tilting of trees and the development of reaction-wood growth on the uneroded side (Carrara and Carroll 1979). In this case the destruction of cambial cells by erosion, and consequent retardation of growth on that side, is an important additional factor. On the west coast of Canada living redwood's are often tilted by flood waters (Stone and Vasey 1968). Trees respond by intensifying wood production on the under-side (i.e. producing reaction-wood) to form buttress-like supports. Angiosperms in the

EXPLANATION OF PLATE 67

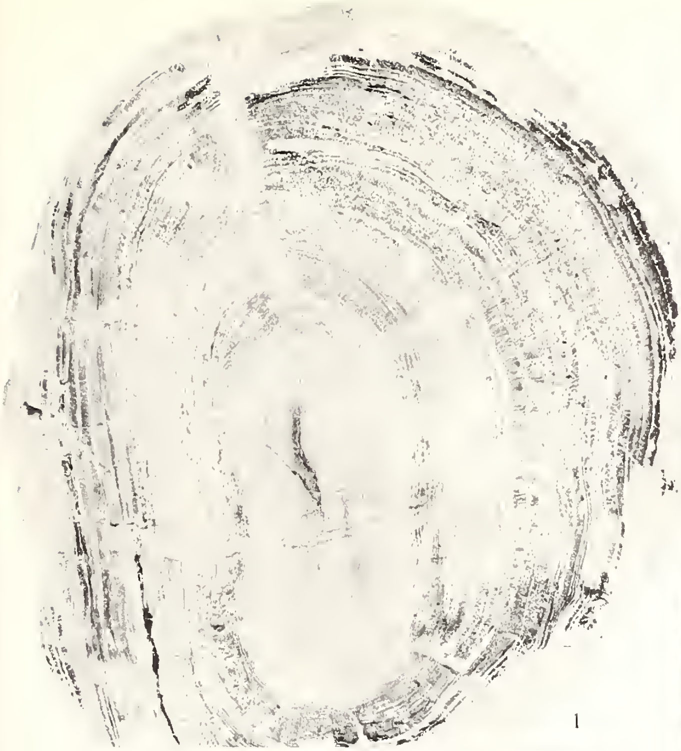
Figs. 1–2. Acetate peels of silicified wood showing general asymmetry of growth. 1, KG.2817.16, ×0·75. 2, KG.2814.252, ×2.

Figs. 3–4. Acetate peels of silicified wood showing reaction-wood. 3, KG.2816.39, ×3. 4, KG.1704.11, ×3.

Fig. 5. Detail from fig. 3, showing rounded cells and intercellular spaces. ×200.

Fig. 6. SEM photograph of helical thickening on the radial wall of a tracheid, KG.2817.15, ×500.

Figs. 7–8. Acetate peels of KG.1704.10. 7, ×0.4. 8, detail ×1.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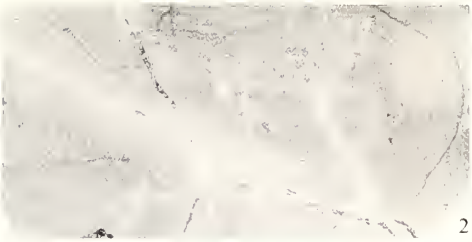
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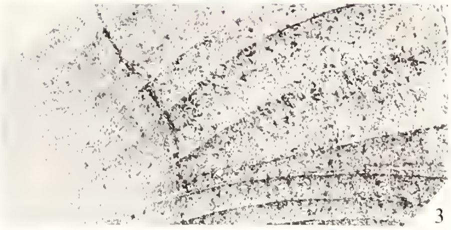
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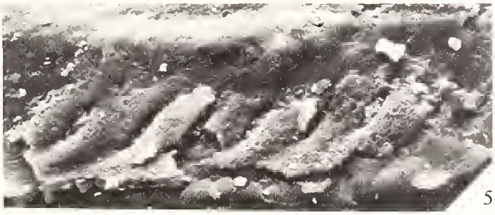
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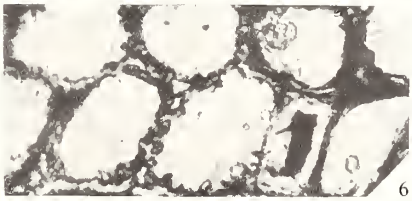
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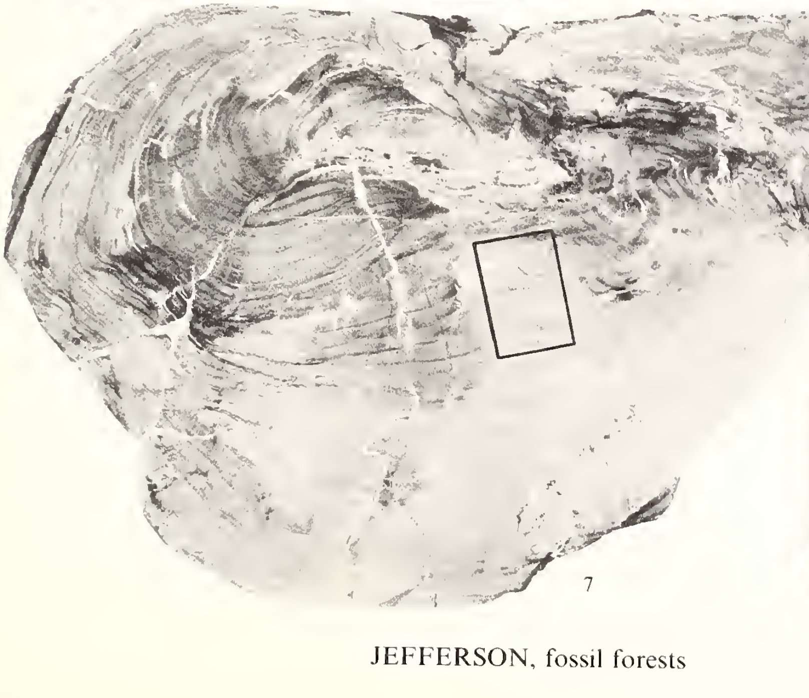
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JEFFERSON, fossil forests

Potomac valley are also frequently bent by flooding (Sigafoos 1964). Growth from inclined trees is generally in the form of vertical shoots regardless of trunk angle. Few gymnosperms exist in this area, so that their behaviour under these conditions is unknown. It is also likely that changes in the intensity and effective direction of light, due to removal of competitors, influence the response to tilting.

Sedimentological evidence from Alexander Island, together with the survival and retardation in growth of trees, strongly suggests that the forests were buried by rapid influxes of fluvial sediment during flooding. Consequent tilting of trees is the most likely cause of the abundant reaction-wood. Several of the trees found in growth position are obviously tilted. The tree in Plate 66, fig. 2 is curved, with its base inclined to the bedding at an angle of 80-85 degrees, and the upper trunk approximately perpendicular. This suggests a recovery from tilting by reaction-wood growth. The tree shown in Plate 66, fig. 3 also tilts slightly and reaction-wood associated with the under-side has been found. Calculation of short-term sedimentation rates using flood-induced reaction-wood, together with palaeosol development, may be possible after further rigorous sampling.

Recognition of tree-rings

Ring-widths were measured directly from acetate peels of specimens cut at 90 degrees to the axis of tracheids. These transverse surfaces were polished and etched in 10% hydrofluoric acid for 165-250 seconds, depending on the amount of carbon remaining in the cell wall. Densitometer and other automatic techniques (see Polge 1969; Fritts 1976) proved unsatisfactory for the measurement of tree-rings because of variations in the quality of preservation (Pl. 68, fig. 3) and because of the occurrence of false rings and crush zones. False rings are easily recognized under the microscope and are discussed below. Pre-petrifactional compaction leads to the development of crush zones within rings, which could be mistaken for ring boundaries (Pl. 68, fig. 1). Microbial degradation and relative cell thickness are important in determining the form and extent of crushing. Since they have very small wall : lumen ratios, early-wood cells are often deformed preferentially, whereas late-wood cells have much thicker walls and therefore greater strength (Pl. 68, fig. 2). In many cases, the reduction in width caused by crushing can be estimated accurately and the ring can be used to build up a ring sequence.

Growth rings in the Alexander Island wood are extremely well defined (Pl. 68, figs. 3-6) and indicate marked seasonality. The cells at the beginning of each ring are invariably large (up to 100 μm in diameter) and thin-walled (Pl. 68, fig. 6). These represent cells which have developed under good growth conditions. Ford, Robards, and Piney (1978) explained the formation of cells in conifers (specifically *Picea sitchensis*) as a progressional development involving 1, cell production by division of active cambial cells; 2, cell expansion; 3, wall thickening; 4, maturation of cells. At a time when cell division is rapid cells join the development 'queue' more quickly and spend longer in the expansion phase. Cells at the end of the rings are small and very thick-walled. These are the products of very slow cell division. Ford *et al.* (1978) considered that the transition to late-wood production was brought about by conditions of low light- or water-availability leading to a low photosynthate supply. Experimental evidence reviewed by Fritts (1976) and Creber (1977), however, indicates that cell division is controlled by the concentration of endogenous growth substances. Gibberelic acid has

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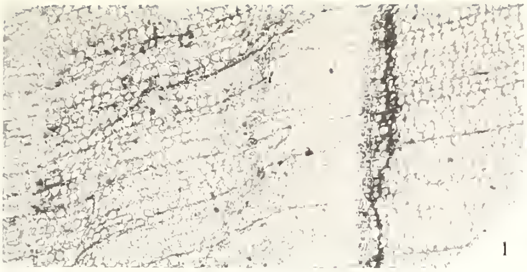
EXPLANATION OF PLATE 68

Figs. 1-2. Acetate peels of deformed cells. 1, KG.1702.2, × 20. 2, KG.2817.16, × 40.

Fig. 3. Growth-rings and densitometer trace showing anomalous density fluctuations in the poorly preserved central part of the large growth-ring, KG.2814.70, × 20.

Figs. 4-7. Growth-rings. 4, KG.2821.98, × 30. 5, KG.2814.254, × 40. 6, KG.1702.2, × 200. 7, KG.2814.254, × 100.

Fig. 8. False ring, KG.2814.252, × 20.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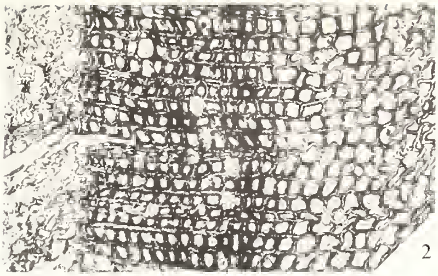
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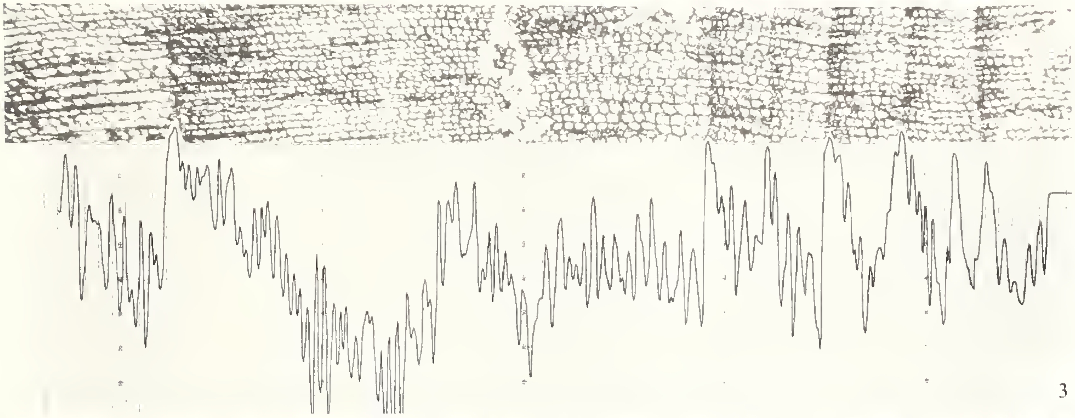
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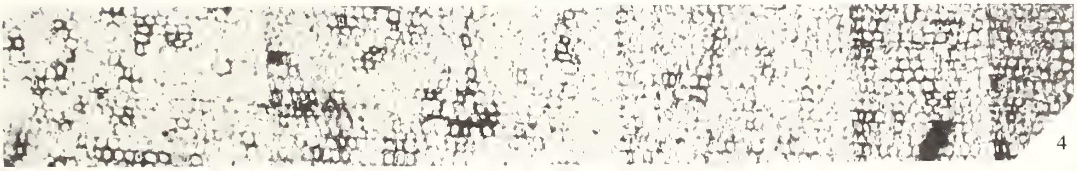
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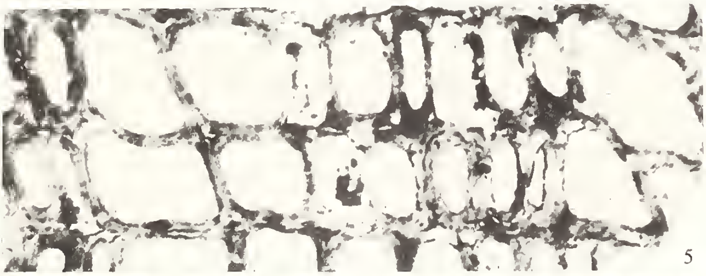
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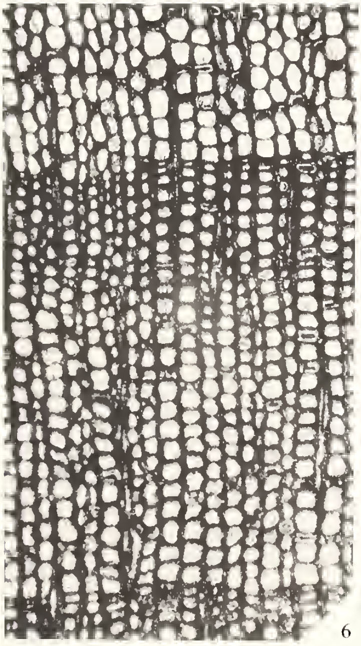
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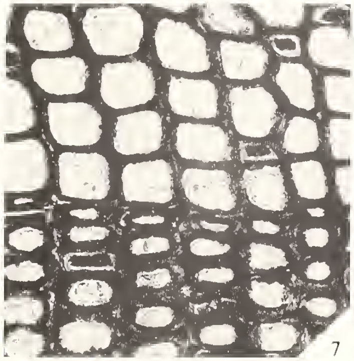
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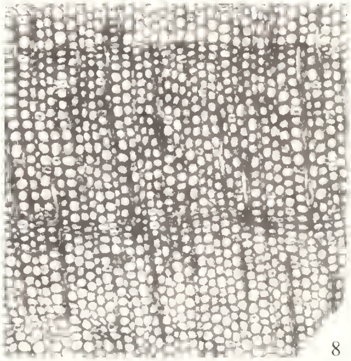
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been shown to stimulate cambial division, while indoleacetic acid promotes differentiation of cells into xylem. It is the concentrations of these, plus several other auxins, which control the change from early- to late-wood production, and the small size of the late-wood cells. It has been demonstrated that the concentration of these auxins is very closely linked to environmental factors, particularly photoperiod (Chaloner and Creber 1973, and references cited). In the Alexander Island fossil woods, decrease in cell size and cell wall : lumen ratio is very gradual throughout each growth ring until both parameters decrease rapidly in the last 3–5 cells (Pl. 68, figs. 2–4). This late-wood zone of small, thick-walled cells is confined to 3–5 cells regardless of the overall size of the growth ring. The boundary between the late wood of one ring and the early wood of the succeeding ring is very well marked (Pl. 68, figs. 5–6). Once the level of auxins present within the trec fell below the threshold which controlled cell division and expansion, a maximum of 3–5 late-wood cells were produced.

False rings

Growth rings, which represent pauses in growth independent of, or in addition to, the main growth pattern, are easily recognized. The gradual decrease in cell size is not followed by an abrupt size increase, but by a gradual transition back into large thin-walled cells (Pl. 68, fig. 7). Furthermore, 'false' rings are far less continuous around the circumference of trees than the 'true' seasonal rings.

The palaeoclimatological significance of false rings is unclear. In different species, and in different environments, adverse environmental conditions can retard growth during the growing season. Drought and frost (Glock 1951) and insect attack (Koerber and Wickman 1970), are the main causes of false rings. Sedimentological and floral evidence strongly suggests that the climate of Alexander Island was not arid (see Jefferson 1981). Almost all the deposits were water-lain, and there is evidence of widespread flooding. Shallow lake deposits bear no evidence of desiccation such as mud-cracks, evaporite minerals, or pseudomorphs. The flora is abundant and diverse and none of the species displays any xeromorphic characteristics (e.g. fleshy leaves with thick cuticle, prickly stems, etc.). Pteridophytes are dominant in many assemblages and common in all. These, particularly the broad net-veined *Hausmannia*-like leaves, are unlikely to have been able to survive periodic drought (Kobayashi 1942). The preservation potential of evidence of insect attack is very low. There is one very well preserved case of fungal attack, which may have exploited insect damage. No insect remains silicified within tracheids, or partially eaten leaves, were found, but this sort of external control cannot be entirely ruled out. In view of the probable palaeolatitude of the fossil forests (65–70° S.) frost during the growing season is a possibility. The implications and difficulties raised by this deduction are discussed below.

False rings can also be produced by stimulating growth at the end of a growing season. This happens when nearby competitors are removed, thus raising the amount of effective available light back above the threshold at which growth is stimulated. Page (1970) described an example of this phenomenon brought about by fault movements. Large-scale flooding may have had the same effect on trees in Alexander Island. Several of the false rings do occur at the end of seasonal rings (Pl. 68, fig. 7).

Significance of tree-rings

In almost all modern trees from temperate latitudes, each ring represents an annual increment of growth (Chaloner and Creber 1973). V. C. LaMarche (pers. comm.) regarded rings which are as clearly defined as those in the Alexander Island woods as annual, regardless of the dominant environmental control. Non-annual growth rings are usually drought-controlled and are much less well defined, with diffuse boundaries (LaMarche *et al.* 1979; Cook and Jacoby 1979). Drought control on growth in Alexander Island is extremely unlikely (see above). Defoliation of trees by insects, which has been discussed, can be a secondary environmental control, but this would shorten the annual ring, or produce a recognizable false ring. Plate 68, figs. 2–6 compare very closely with the undoubtedly annual growth rings of larch trees (Schweingruber 1979, figs. 2 and 6), which have very similar cell patterns, densitometer traces, and false rings.

TREE-RING ANALYSIS

Methods

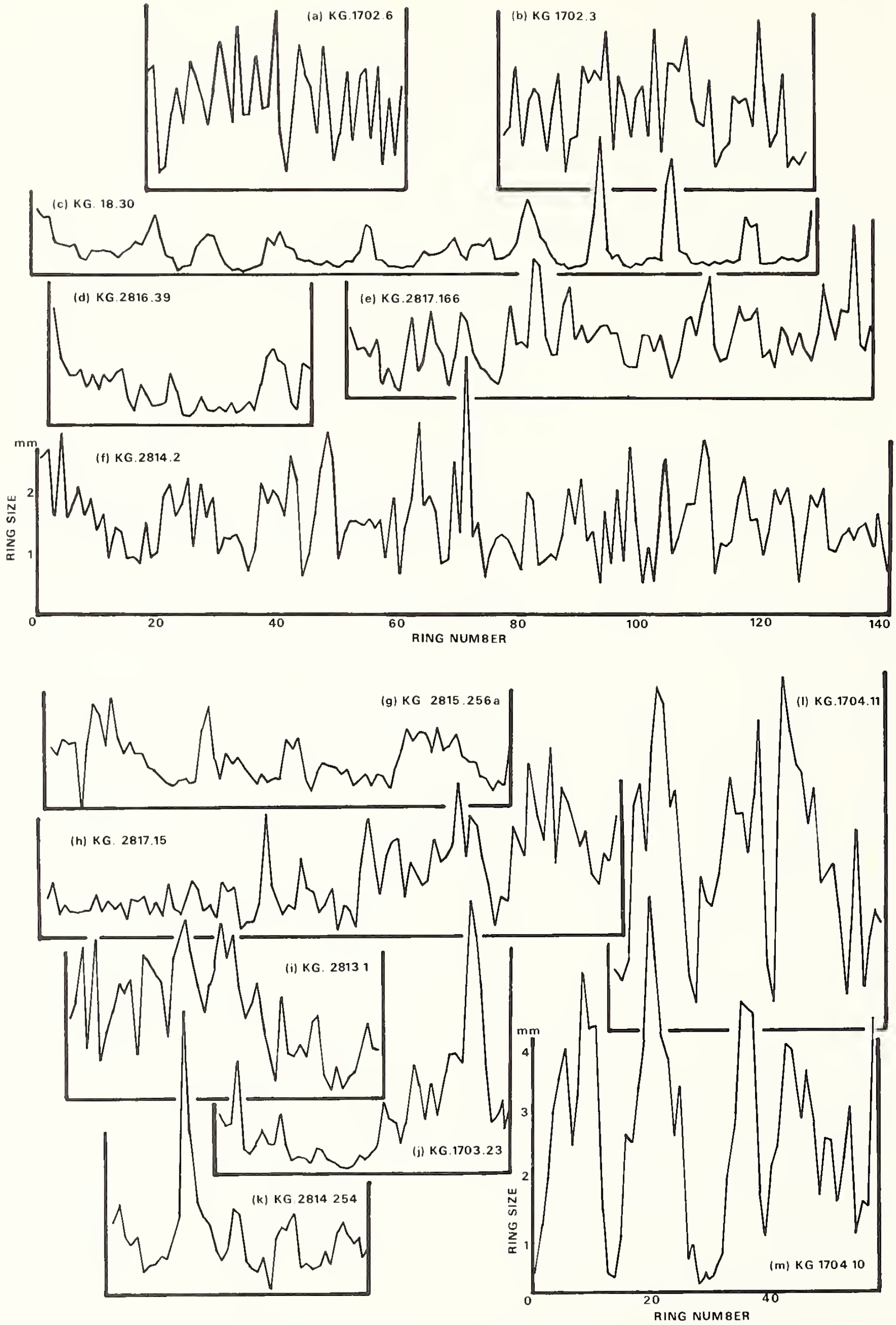
Twenty-seven ring sequences were built up from twenty-one well-preserved trees. The selected specimens all have a continuous sequence of consecutive rings which are not interrupted by areas of poor preservation, or pre-mineralization crushing (e.g. Pl. 67, figs. 7–8). In some cases building up such a sequence involved traversing around the circumference of a ring boundary, for up to 10 degrees, in order to find an area of better preservation.

The data for sequences with more than forty rings are reproduced graphically in text-fig. 6. Table 1 sets out the results of statistical analysis to find the 'mean sensitivity'. This is a statistical measure of variation in annual increments of growth used by dendroclimatologists (e.g. Glock 1955; Fritts and Shatz 1975; Fritts 1976; LaMarche *et al.* 1979). It was devised by Douglass (1928) in order to assess accurately whether a ring sequence was 'complacent' or 'sensitive'.

TABLE 1. Results of statistical analyses of tree-ring data showing mean sensitivity and mean and maximum ring-widths.

Locality	Specimen number	Number of Rings	Mean Sensitivity	Standard Deviation	Mean ring-width	Standard Deviation	Maximum ring-width
Georgian Cliffs	KG.18.25a	18	0·739	0·474	1·144	1·048	3·80
	KG.18.25b	23	0·535	0·405	1·269	1·114	4·24
	KG.18.30	130	0·338	0·351	0·401	0·342	2·27
Hyperion Nunataks	KG.1702.2	29	0·029	0·050	0·980	0·083	1·12
	KG.1702.3	53	0·528	0·410	1·340	0·665	2·77
	KG.1702.6	43	0·621	0·378	1·503	0·684	3·00
Triton Point	KG.2813.1	52	0·422	0·331	1·496	0·784	3·02
	KG.2813.15	33	0·415	0·367	1·262	0·826	3·90
Coal Nunatak (north)	KG.1703.23	49	0·404	0·269	0·993	0·928	4·52
	KG.2814.2	141	0·393	0·310	1·510	0·613	4·24
	KG.2814.254	43	0·404	0·361	0·959	0·733	4·70
Coal Nunatak (south)	KG.2815.71	34	0·326	0·278	1·161	0·736	4·24
	KG.2815.256a	77	0·373	0·376	0·751	0·379	1·81
	KG.2815.256b	38	0·434	0·333	1·309	0·794	3·33*
Titan Nunatak (east)	KG.1704.10	58	0·468	0·383	2·517	1·595	6·85
	KG.1704.11	45	0·421	0·401	2·941	1·500	5·85
	KG.2816.39a	44	0·408	0·318	0·582	0·360	1·83
	KG.2816.39b	14	0·430	0·290	1·094	1·016	4·23*
	KG.2816.39c	37	0·339	0·236	0·557	0·315	1·49
	KG.2816.40	38	0·418	0·352	1·594	0·921	3·93
Titan Nunatak (west)	KG.2817.15	96	0·443	0·315	1·080	0·874	3·12
	KG.2817.16a	68	0·492	0·478	0·849	0·597	2·21
	KG.2817.16b	88	0·423	0·330	0·980	0·487	2·91
Pagoda Ridge	KG.1719.3a	19	0·420	0·311	3·581	1·785	7·78
	KG.1719.3b	20	0·442	0·391	2·309	1·560	7·42
	KG.2821.97	13	0·393	0·314	1·620	0·633	2·73
	KG.2821.98	21	0·403	0·292	1·934	0·963	3·96

* = Reaction-wood



TEXT-FIG. 6. Plots of growth-ring sequences used in statistical analyses.

The 'annual sensitivity' is the difference in width of each pair of consecutive rings divided by their mean width:

$$\text{Annual sensitivity} = \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|$$

$$\text{and Mean sensitivity} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_t + x_{t+1}} \right|,$$

where x is the ring-width, t is the year number of the ring, and n is the number of rings in the sequence. A modification of the formula (Schulman 1956; Furst 1963) which simplifies calculation was rejected by Creber (1977) and by other workers in the field as it is necessary to discard data from the first fifty rings. Trees with mean sensitivities above 0·3 are by convention sensitive, and those with values below 0·3 are complacent.

Results

The results set out in Table 1 show 1, consistently high mean sensitivities of most of the trees; 2, high mean ring-widths; and 3, very high maximum ring-widths.

The data fall into two groups based on mean sensitivity, one with very variable (mean 0·463, standard deviation 0·249), and the other with consistent (mean 0·411, standard deviation 0·039), mean sensitivities. The first group consists of wood from Georgian Cliffs (KG.18) and Hyperion Nunataks (KG.1702) (text-fig. 1). At both localities the wood is clearly drifted. At Georgian Cliffs the wood occurs in marine rocks and much is heavily bored by marine bivalves. At Hyperion Nunataks the facies is uncertain, but no standing trees or stumps have been found and rare and fragmentary leaf fossils indicate a drifted flora. The assemblages from these localities appear to be mixed, with wood from both very sensitive and complacent trees. All the wood at the second group comes either from beds containing *in situ* forests or from beds close to these forests, and the tree-rings indicate no environmental changes throughout the time period, or over the geographical area represented by the southern part of the Fossil Bluff Formation. The distribution of annual sensitivities also shows a distinction between the two groups (text-fig. 7). The annual sensitivities of the wood in the 'drifted' assemblages are dominated by low values ($< 0{\cdot}1$) but have a number of very high values, whereas the mode of the '*in situ*' sensitivities is 0·2–0·3 and the distribution is much less skewed.

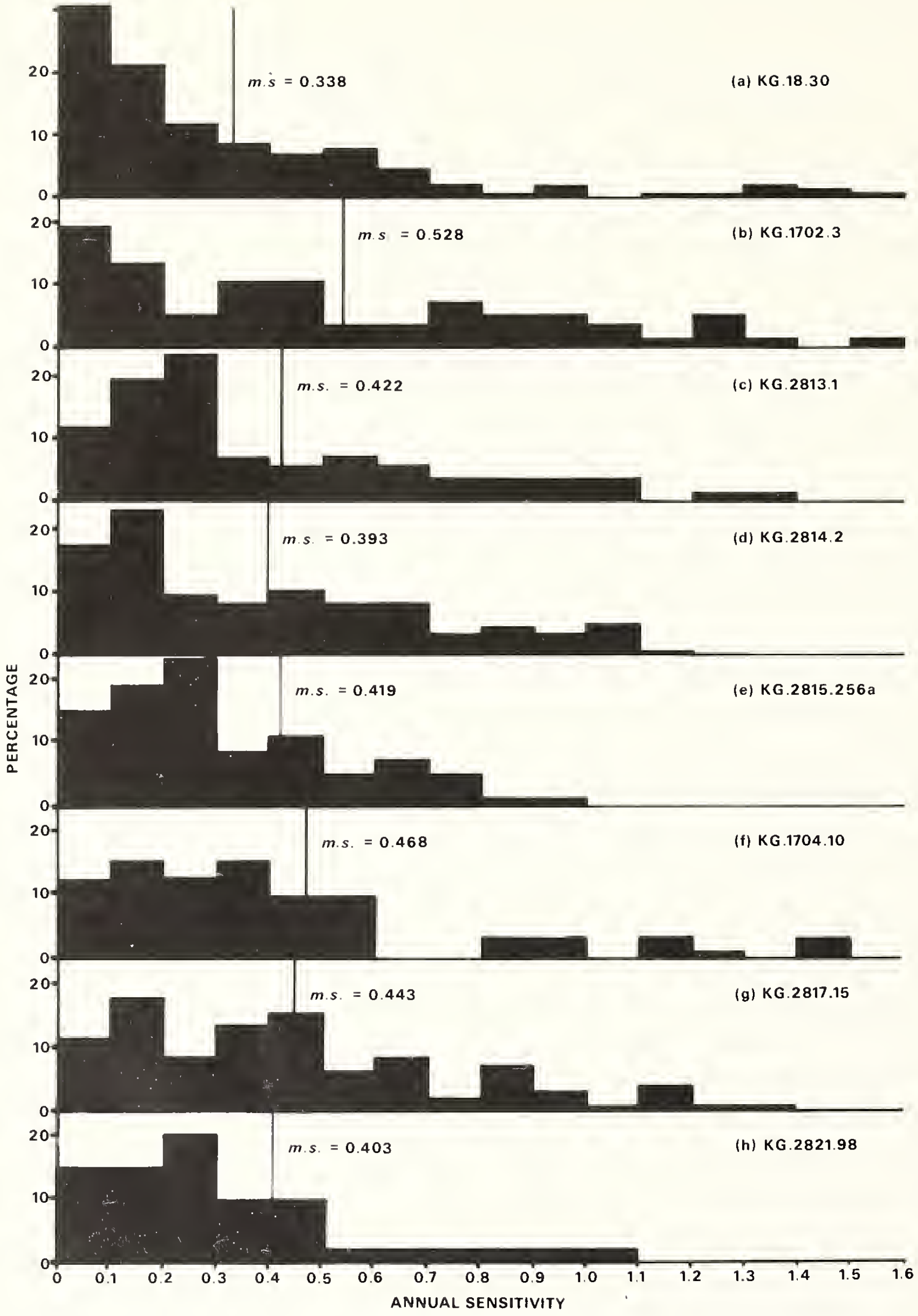
The mean ring-widths and maximum ring-widths are far less consistent because samples inevitably come from different parts of trees. Some of the sequences probably come from branch material (e.g. KG.2815.256). Others were taken from the suppressed parts of reaction-wood (e.g. KG.2816.39). However, many of the trees show very high mean ring-widths, often well above 2 mm (Table 1). The largest ring recorded is 9·55 mm across (Pl. 67, fig. 7) and 50% of the *in situ* group bear rings in excess of 3·9 mm (Table 1).

Comparisons with living trees

Modern sensitive trees are almost entirely confined to marginal environments. When a tree is growing close to the limits of its ecological range any fluctuation in the climatic limiting factor will be reflected in the growth ring laid down that year. The only conifers which consistently show mean sensitivities near to, or above, 0·4 are those growing in a semi-arid environment, where it is variation in water availability which is reflected in the growth rings (Fritts and Schatz 1975). In such environments in western North America mean sensitivities of 0·6 have been recorded (Schulmann 1956 and data in Schulmann processed by Creber, pers. comm.). As stated above, however, all the sedimentological and floral evidence points to a humid climate during the deposition of the Fossil Bluff Formation.

In other marginal environments for conifer growth (high altitude and high latitude) growth is controlled by temperature or day length. LaMarche and Stockton (1974) found that bristle-cone pines at the upper tree-line were not sensitive. Mean sensitivities of trees from the nine sites in the Great Basin and Colorado–New Mexico areas range from 0·12 to 0·26 with a mean of 0·19. In contrast, bristle-cones from the lower forest border give a mean sensitivity of 0·43.

The most comprehensive data for trees at the sub-Arctic tree-line come from Alaska, northern Canada, and northern Norway, though tree-ring data from other sub-Arctic zones are closely comparable (Adamenko 1963). In Alaska, Giddings (1943), Andersen (1955), and Garfinkle and



TEXT-FIG. 7. Histograms allowing comparison of variation in the annual sensitivities from eight of the fossil trees. E.g., in (*a*) 31% of the annual sensitivities have values less than 0·1, 20% have values between 0·1 and 0·2, etc.

Brubaker (1980) emphasized the dominance of growing-season temperatures in the control of growth in sub-Arctic trees. Important features of the trees from Gidding's (1943) spruce tree-line sites (69° N) are the low mean and maximum ring-widths, which at the site giving the highest values are only 0·9 mm and 2·2 mm, respectively. Ording (1941) found that late May temperatures were the major control on growth at the northern Norwegian tree-line and that even in this marginal environment the trees were complacent. An analysis, in 100-year blocks, of Ording's (1941) 530-year ring-sequence from fifteen trees in lat. 58° N gives an overall mean sensitivity of 0·1489 and a maximum of 0·1795. Mean ring-widths are again small, 0·54 mm at the tree-line, and less than 1 mm at 60° N. The largest ring for any tree north of 60° is 2·05 mm.

Data from northern Canada (Drew 1975) also indicate low sensitivity at the northern tree-line. The highest mean sensitivity for any sub-Arctic site is 0·1999 at lat. 68° N and the average for nine such sites north of 60° is 0·163. Mean and maximum ring-widths are again low, approximately 1 mm and 1·87 mm, respectively. Dimensions given by Riley and Young (1974) indicate that in Labrador Sitka spruces commonly have mean ring-widths as low as 0·35 mm.

Conclusions

Any analogy between high latitude climatic regimes today and those operating in similar latitudes during the early Cretaceous is clearly untenable. In interpreting the climatic type which is most likely to have produced the tree-growth patterns observed in the Alexander Island fossils, there is a further complication. Work by LaMarche (in press) suggested that, to a certain extent, growth patterns may be genetically controlled. Even in a marginal environment, where climate strongly influences growth, only sensitive species of trees will give high mean sensitivities. This is highlighted by the work of Dunwiddie and LaMarche (1980) on *Widdringtonia cedarbergensis*, from a marginal site in the Cedarberg Mountains of South Africa. Despite a very close correlation between growth and climate (75% of variation in growth-ring size is accounted for by variation in temperature and rainfall), the mean sensitivities of the trees is only 0·15 (LaMarche *et al.* 1979). In contrast, data on the genus *Phyllocladus* (celery top pine) from southern New Zealand and Tasmania show that these very sensitive trees reacted strongly to environmental fluctuations in a less marginal environment. These primitive podocarps grow between latitudes 35° and 44° S in temperate rain forests on humic soils. LaMarche *et al.* (1979) analysed trees in the genus *Phyllocladus* at fifteen sites and found that the mean sensitivities were consistently high. Although the average was 0·32, three sites gave values in excess of 0·4 and one in excess of 0·5. Mean ring-widths were up to 1·47 mm and the largest ring index was 2·32 mm. Since the ring indices for each site are compiled from four to twenty-three trees, many individual trees will have considerably higher maximum ring-widths. The similarity of the growing patterns of the Alexander Island fossil trees to those of living *Phyllocladus* indicates that they grew under conditions much closer to those found in present-day warm–temperate rain forests than to those found in high latitude regions.

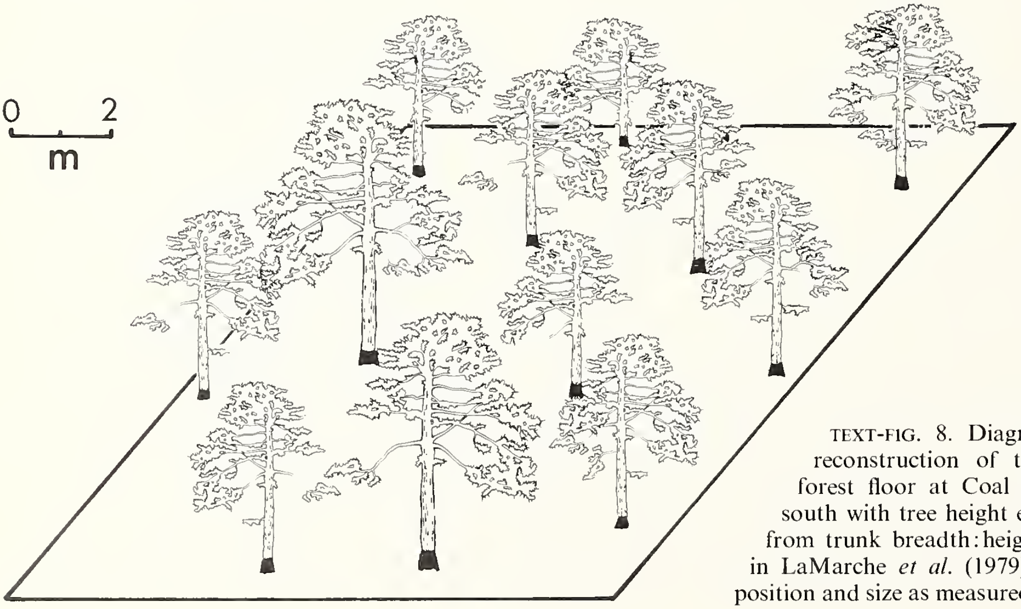
The rapid growth rates indicated by the mean and maximum ring-widths would be very high for modern conifers even at low latitudes. However, the environmental range of the conifers is influenced to a large extent by the distribution of the angiosperms, and climatic controls in operation today are unlikely to be an accurate reflection of those during the Cretaceous. One factor which is widely believed to have remained constant during this period is the solar constant (see Foukal 1980 and references therein). Bearing this in mind, the amount of solar energy received at a latitude equivalent to south-east Alexander Island in the lower Cretaceous would be sufficient to sustain tree-growth. Twenty-four-hour daylight during at least part of the growing season might be expected to stimulate production of growth-promoting hormones. Photoperiod has been proved experimentally as the major control on these auxins (Larson 1956; Fritts 1976; Creber 1977). Ford *et al.* (1978) found that cell division could take place only if trees received more than 15 mJ m^{-2} d^{-1}. Data on solar energy received at sites close to the Antarctic circle today (Farman and Hamilton 1978) suggest that a growing season of five months could be sustained at these sites, but substantial growth would be limited to two months. The harshness of the winter and high frequency of frost during the growing season preclude the colonization of polar regions by modern trees capable of rapid growth. Although these may not have been in operation during the Early Cretaceous, the low availability of light would restrict tree-growth. Furthermore, the low angle of incidence of the sun's rays would lead to extreme problems of shading in dense forests. Even at midday of the summer solstice the sun is at an elevation of only 48·5°, and two months either side of this the elevation is 27°. Text-fig. 8 shows the arrangement of the fossil forest floor at Coal Nunatak south (KG.2815). Although the trees are spaced widely enough to survive, the length of the growing season would be reduced, together with the number of hours per day with effective sunlight. Ground-dwelling vegetation, of which there is considerable evidence, would also be shaded out by this tree cover.

PERIODICITY OF TREE GROWTH

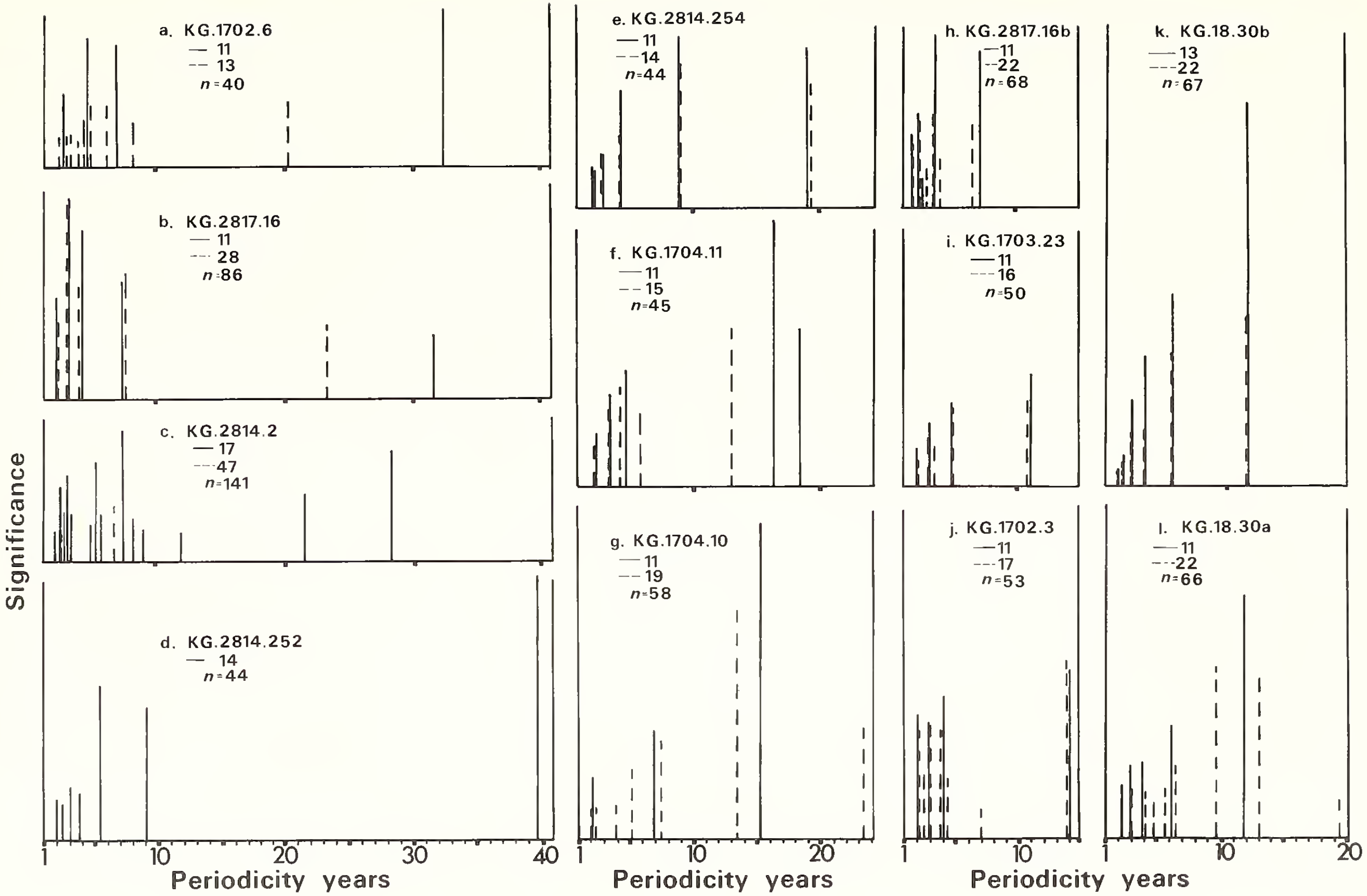
Methods

All tree-ring sequences with over forty rings were analysed for significant periodicities in their growth patterns. Strongly periodic growth can be picked up visually from graphical representation of the data. The regular repetition of peaks in text-fig. 6*c* suggests a periodicity of between ten and twelve years in specimen KG.18.30. However, in most cases periodicities are smaller and are masked by interaction with other periodicities (text-fig. 6*f*), and can only be discovered by mathematical analysis. The computer program used was Maximum Entropy Spectral Analysis (MESA) (Ross 1975), which for short lengths of data has a resolution superior to other methods

The effect of any stimulus on tree-growth in a given year will affect growth in subsequent years. Thus a particularly short, cold, growing season will produce a small growth-ring, but its effects will be seen in the next few rings. As a result, the growth-ring for year n will correlate very closely with that for year $n+1$ and progressively less well with years $n+2$, $n+3$, $n+4$, etc. This is likely to mask the effect of periodic growth. The first part of the program analyses this autocorrelation due to the lag effect of climatic stimuli, and removes it from the raw data. Such autocorrelation in the Alexander Island fossil trees is very low and rarely significant beyond $n+1$. The data are then processed by searching for periodicities within sections of the series using a 'window' through which a fixed number of data poits are analysed. The window then moves on one point, repeats the analysis, and so on until the end of the series. The program uses a range of window-widths from one data point to one-third of the number of data points, selects the one which reveals the clearest periodicities, and gives the results of this analysis together with that using the highest window-width. The results for each ring-sequence are reproduced graphically in text-fig. 9.



TEXT-FIG. 8. Diagrammatic reconstruction of the fossil forest floor at Coal Nunatak south with tree height estimated from trunk breadth:height ratios in LaMarche *et al.* (1979). Stump position and size as measured.

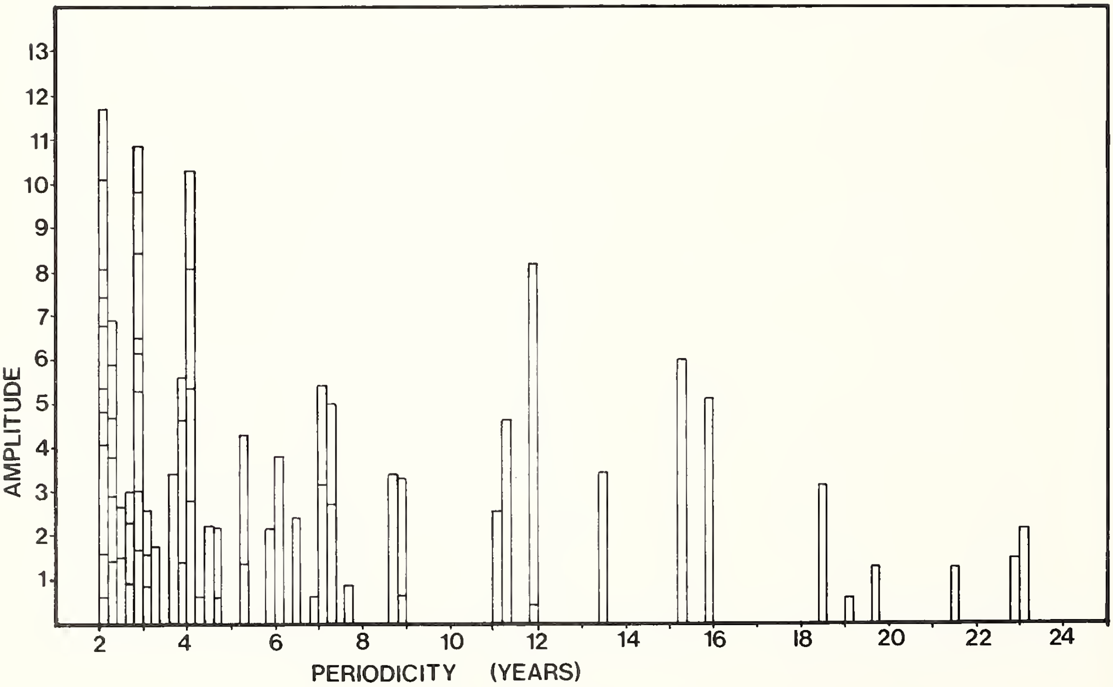


TEXT-FIG. 9. Periodicity of growth from individual trees against amplitude as measured by MESA (see text, p. 702, for explanation). Solid lines = periodicity found using lower filter coefficient. Broken lines = periodicity found using coefficient N/3.

In most cases use of the greatest window-width picks out the same periodicity as use of the optimum width (e.g. text-fig. 9*e*, *i*-*k*); in others it replaces some periodicities recognized by the optimum window with two less significant periodicities with similar frequencies (text-fig. 9*f*, *l*). In most cases it emphasizes the lower frequency periodicities (e.g. text-fig. 9*g*, *j*, *l*). The ring-sequence for KG.18.30 was run in two halves. The use of the optimum window-width on the first half of the sequence produced an eleven-year periodicity which was 'split' by the use of the greatest window-width. This periodicity was much more prominent in the second half of the data (the second half of the tree's life) and was not 'split' when a larger window was used.

Results and discussion

A histogram combining periodicities shown by all the trees analysed is shown in text-fig. 10. Two-, three-, and four-year periodicities are shown by most of the trees analysed. These may be purely biological in origin or may be related to the biennial or triennial solar cycles (Schove 1978). LaMarche and Stockton (1974) and Schove (1978) found 2·2- and 3·3-year cycles in ring-sequences from living trees. A very strong eleven- to twelve-year cycle is present in four of the trees (KG.18.30; KG.1704.10, 11; KG.2814.2) and is probably externally controlled. Although the interpretation of such a small data base from a localized area must be treated with caution the well-documented sunspot cycle (eleven and twenty-two years) is one possible cause of tree-growth periodicity which could be considered. Eddy (1976) showed that greatly reduced sunspot activity (the 'Maunder minimum') coincided with a 'little ice age' between 1645 and 1715. Stuiver and Quay (1980) found that the proportion of ^{14}C in tree-rings corresponded closely to sunspot cycles and demonstrated that three other cold periods since AD 1000 coincided with low sunspot activity. Few living trees show any eleven- or twenty-two-year periodicity (Monin and Vulis 1971; LaMarche and Fritts 1972), though Erlandsson (1936) found an eleven-year periodicity (amongst others) in pines from northern Sweden, and Bitvinskas (1971) reported a strong correlation between tree-growth and the twenty-two-year



TEXT-FIG. 10. Compilation of periodicities and amplitudes for all trees. Each 'block' represents data from one tree.

solar cycle in Lithuanian pines. The effect of sunspots on climate probably relates to the increased short-wave radiation at sunspot maxima. This radiation causes reactions producing nitrogen oxide and ozone which increase the albedo of the atmosphere (Foukal 1980) but Kondratyev and Nikolsky (1970, 1979) suggested that the mechanisms are more complex.

In climatically sensitive trees like those growing on Alexander Island during the Early Cretaceous, an eleven-year periodicity of growth may be induced by sunspot-related climatic fluctuation. More data from a wide range of areas and time periods will be necessary in order to fully test this hypothesis.

A strong seven-year periodicity is present in at least five of the fossil trees (KG.1704.10, KG.1702.3 and 6, KG.2814.2, and KG.2817.16). This may relate to volcanic dust in the atmosphere after a major volcanic eruption (Chance and Kelly 1979). Volcanic activity in the nearby volcanic arc may have had an effect on climatically sensitive vegetation in the Alexander Island area. Although the destructive effects of ash clouds on forests immediately surrounding a volcano have been dramatically demonstrated by the recent eruption of Mount St. Helens (Fritz 1980*b*), the long-term effect on trees outside the area of destruction is not fully understood.

CONCLUSIONS

1. In the Early Cretaceous, conifer forests grew in Alexander Island. The characteristics of these forests (see 2–5) are apparently inconsistent with the approximate palaeolatitude (70° S) in most palaeogeographical reconstructions.

2. Silicification depended on rapid burial of trees in coarse volcaniclastic sediment and early release of silica during diagenesis. Flask-shaped bases and reaction-wood developed as a result of inundation by water and sediment influx.

3. Analysis of tree-rings indicates rapid growth rates, high climatic sensitivity, and seasonality of growth. These are characteristics of some trees growing in warm-temperate climatic regimes with long growing seasons.

4. The trees were closely spaced. If the angle of incidence of the sun's rays was the same as at similar latitudes today, this would further reduce the amount of available light (and therefore the length of the growing season) by shading.

5. Growth patterns show strong two-, three-, four-, seven-, and eleven-year periodicities. This suggests that the biologically induced high-frequency growth cycles found in living trees operated during the Early Cretaceous. It also implies the existence of external periodic controls on growth, such as sunspot activity and volcanic dust in the atmosphere.

6. The apparent inconsistencies between geophysical and palaeobotanical evidence are supported by the evidence from leaf floras from the same area (Jefferson 1981). There are four possible explanations for these inconsistences:

(*a*) It is possible that reconstructions of the local palaeogeography of Lesser Antarctica are incorrect. The Antarctic Peninsula may have been displaced to the north and situated west of South America (e.g. Harrison, Barrow, and Hay 1979), or its eastern margin may have been situated parallel to the Falkland Plateau (text-fig. 2). However, even in these unlikely cases the 110 ma palaeolatitudes are 60° and 66° S respectively.

(*b*) Today, no polar land areas are maintained at high temperatures during the polar night by the influence of globally high sea temperatures. Any sort of uniformitarian approach to palaeobotanical interpretation may, therefore, be incorrect; no vegetation adapted to such an environment exists today. The remarkable similarity of wood structure between the fossil trees and living trees, and considerations of functional morphology, suggest that this is unlikely.

(*c*) One or more of the basic assumptions inherent in any palaeogeographic reconstruction may be incorrect. Palaeomagnetic data fix continental positions relative to the magnetic pole and it is possible that over long periods of time this may not relate as perfectly to the geographic pole as present geomagnetic theory suggests.

(*d*) The earth's geographic poles are assumed to have been orientated at the same angle to its axis of rotation around the sun (23·5°) throughout geological time. Recent theories (e.g. Williams 1974) suggest that this may not be the case and that, during the Early Cretaceous, the angle was between ten and fifteen degrees. This would move the polar circles and all other climatic belts approximately ten degrees poleward in terms of photoperiod.

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A NEW RHYNCHOCEPHALIAN FROM THE BRITISH UPPER TRIAS

by N. C. FRASER

ABSTRACT. The skull of a new fossil reptile, *Planocephalosaurus robinsonae* gen. et sp. nov., is described and its affinities discussed. The description is based on approximately 750 isolated skull bones recovered from Triassic fissure infills in Carboniferous Limestone in the Bristol Channel area. The skull is diapsid, although there is usually a small gap present in the lower temporal bar. Further evidence that an incomplete lower temporal bar is not a uniquely squamate character is provided. The new reptile is compared with the eosuchians and the taxonomic position of the family Sphenodontidae is reviewed.

CROMHALL QUARRY is one of several localities in the Bristol Channel area that yielded a fauna of Triassic terrestrial vertebrates (Robinson 1957). The fossils mostly occur in the sediment fills of karstic fissures and cave systems close to the Carboniferous Limestone/Triassic unconformity. The sediments consist of marls, sand, and recemented limestone debris, and most research has hitherto been directed towards articulated specimens of reptiles that have been recovered from the marls. More recently, however, Halstead and Nicoll (1971) drew attention to dissociated material within the recemented debris, and it is this that is now being re-investigated.

The recemented material consists mainly of derived crinoid ossicles and fine limestone debris which has been washed into solution features from the surrounding limestone surface. The vertebrate bones have been incorporated into this debris and cemented along with the limestone residues.

Cromhall is the type locality for the sphenodontid *Clevosaurus* (Swinton 1939; Robinson 1973) and reptilian faunas have now been described from six other similar localities in the Bristol Channel area (Robinson 1957). Halstead and Nicoll (1971) listed five groups of reptile from Cromhall, and whilst the present study involving some 1000 identifiable skull elements has revealed only three such groups, at least eight species are represented, of which six may be new. The present paper is a preliminary description of the commonest of these.

Work on the new genus and other genera from the Triassic fissure deposits is now continuing at Aberdeen University funded by a Research Grant through the NERC.

METHODS

Blocks of bone-bearing fissure limestone up to 6 kg are placed on trays within standard washing-up bowls and covered with 5% acetic acid. The acid neutralizes within two to three days and the bowls are then gently flushed with tap water for at least two hours to remove any salts from the residues. Most bones recovered are less than 15 mm long and need no protective treatment during solution. Residues are separated through sieves, dried, and then sorted by hand using fine sable brushes. Plate 69, fig. 5 illustrates a partially developed block and an archosaurian tibia revealed within the matrix.

Whilst a small degree of breakage occurred during recovery, this was insignificant and assemblages reveal that the more delicate elements such as nasals and prefrontals are under-represented in comparison with the robust bones, for example the principal jaw elements (Appendix 1). The size range of the bones is considered to be representative of both juveniles and adults. Some maxillae no longer than 3 mm have been recovered showing well-preserved unworn teeth, whilst the largest maxillae are over 12 mm long. In these specimens the teeth are worn and covered by secondary

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dentine. The various skull dermal bones have a corresponding size range, from juvenile stages through to mature forms. In dealing with a mixed assemblage of dissociated bones belonging to several species two lines of approach have been used. First, due note has been paid to the ratios of abundance of the individual skull elements when attempting to identify skull associations for individual species. Whilst variations in these ratios occur from locality to locality and level to level, which may reflect sorting patterns in water or other factors, the overall ratios of skull bones certainly reflect the original relative abundances of the species concerned. The validity of these statistically implied skull associations is then checked by a careful examination of the articulation facets between adjacent elements. This work is now complete for the most abundant skull element association, and these bones have been combined in a reconstruction (text-fig. 1). The association represents a new species of sphenodontid, which, although similar in some respects to *Clevosaurus*, is quite distinct and merits the erection of a new genus.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA
Subclass DIAPSIDA
Infraclass EOSUCHIA
Order RHYNCHOCEPHALIA
Family SPHENODONTIDAE
Genus *PLANOCEPHALOSAURUS* gen. nov.
Species *P. robinsonae* sp. nov.

The generic name refers to the characteristic flat parietal table which is in contrast to the median ridge often found in other genera of the family. The specific name is a testimonial to the work of Dr. Pamela L. Robinson.

Diagnosis. A small sphenodontid, skull approximately 2 cm long; temporal region diapsid but with a small gap normally present in the lower temporal bar, cf. *Clevosaurus*; frontals and parietals fused; a broad and flat parietal table with a large central pineal foramen; no supratemporal or lacrimal; deep overlap of the pterygoid and quadrate; quadrate and quadratojugal fused with a quadratojugal foramen present; premaxillae paired; vomers bear small scattered teeth; the pterygoids typically display two tooth rows; no teeth on the pterygoid flange; palatines bear two rows of obtusely conical teeth parallel to the marginal dentition; dentition acrodont; all teeth are radially ribbed; dentary has a posterior process articulating with the articular complex; no splenial.

Material. The description is based on a collection of approximately 750 catalogued skull elements that are housed in the geology department of the University of Aberdeen.

Holotype. Left maxilla. No. 11061 in the University of Aberdeen Palaeontology collection. Plate 69, figs. 1-4.

Type locality. Karstic fissures in Dinantian Limestones. Cromhall quarry, south Gloucestershire.

Horizon. Upper Triassic.

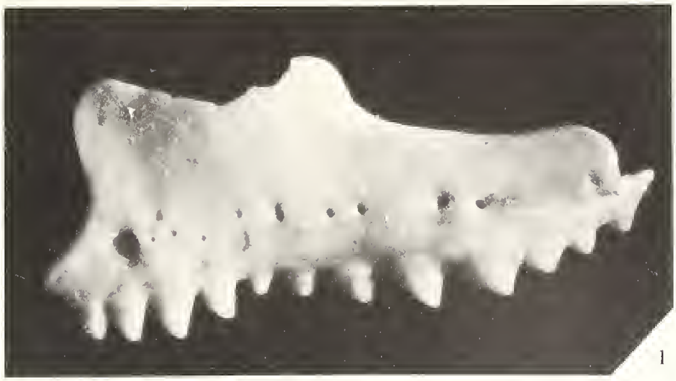
EXPLANATION OF PLATE 69

Figs. 1-4. *Planocephalosaurus robinsonae* gen. et sp. nov. Holotype, left maxilla, No. 11061, Aberdeen University Palaeontology collection. 1, lateral view, × 10. 2, detailed lingual view of the flanged tooth series, × 15. 3, lingual view, × 10. 4, detailed lingual view of the anterior dentition, × 15.

Fig. 5. Archosaurian tibia exposed from a partially developed block of fissure material, $\times \frac{2}{3}$.

Fig. 6. *P. robinsonae* gen. et sp. nov. Detailed lateral view of a dentary, AUP No. 11062, and maxilla, AUP No. 11063, to show the wear facets on the lateral surface of the dentary caused by the maxillary dentition, × 10.

Fig. 7. *P. robinsonae* gen. et sp. nov. Lateral view of a left prefrontal, AUP No. 11064, × 10.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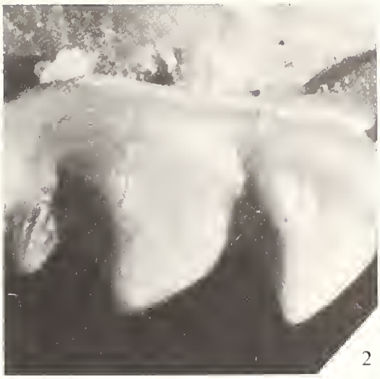
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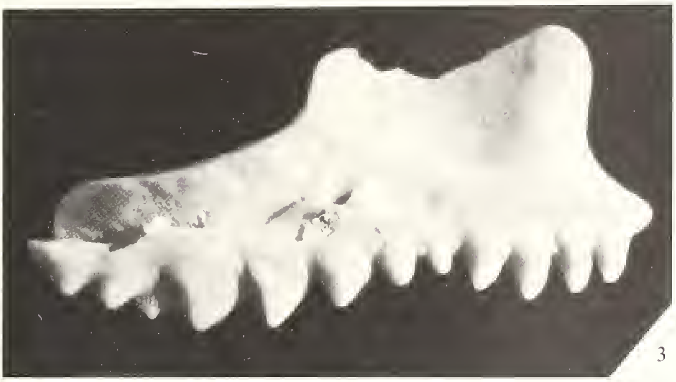
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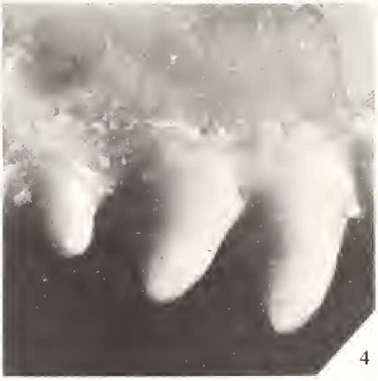
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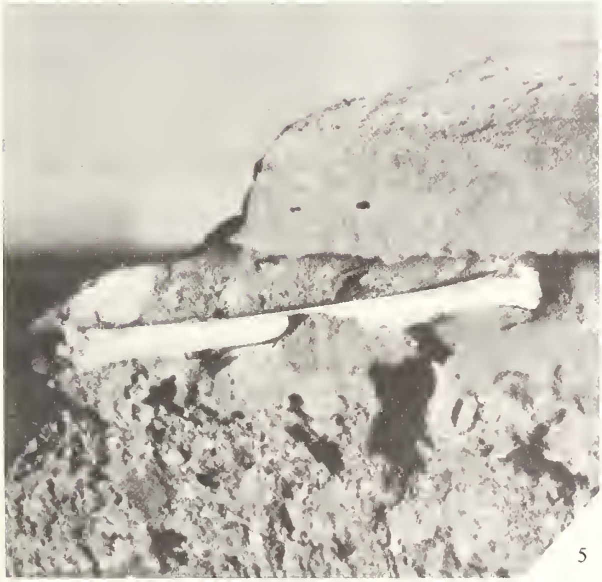
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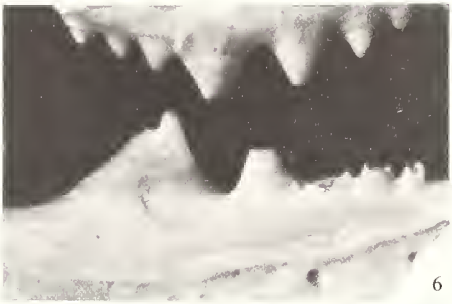
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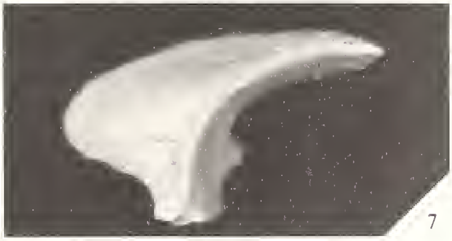
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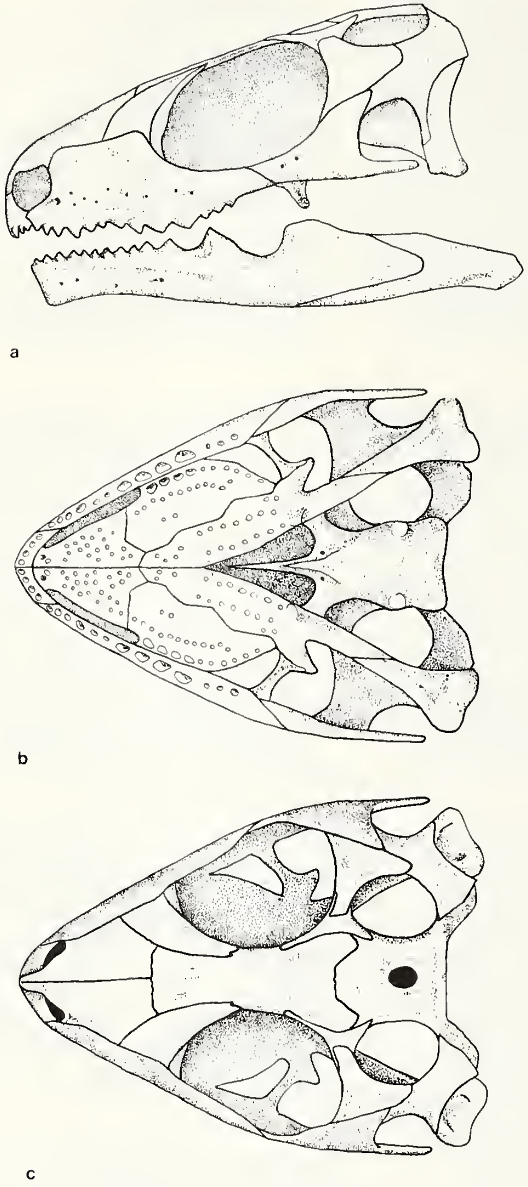
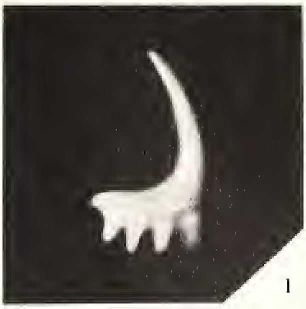
FRASER, *Planocephalosaurus*



TEXT-FIG. 1. *Planocephalosaurus robinsonae* gen. et sp. nov. Reconstruction of the skull in *a*, lateral, *b*, palatal, and *c*, dorsal view.

EXPLANATION OF PLATE 70

Figs. 1–12. *Planocephalosaurus robinsonae* gen. et sp. nov. 1, lateral view of a right premaxilla, AUP No. 11065, × 5. 2, a left dentary, AUP No. 11066, in lateral view, × 5. 3, a left postorbital, AUP No. 11067, in lateral view, × 5. 4, lingual view of a left dentary, AUP No. 11066, × 5. 5, a frontal, AUP No. 11068, in dorsal view, × 10. 6, the lingual aspect of a right jugal, AUP No. 11069, × 5. 7, dorsal view of the left side of a parietal, AUP No. 11070, × 5. 8, ventro-medial aspect of a right quadrate, AUP No. 11071, × 5. 9, lateral view of a right jugal, AUP No. 11069, × 5. 10, dorso-lateral view of a right nasal, AUP No. 11072, × 5. 11, dorso-lateral view of a right postfrontal, AUP No. 11073, × 10. 12, postero-lateral aspect of a right ectopterygoid, AUP No. 11074, × 10.



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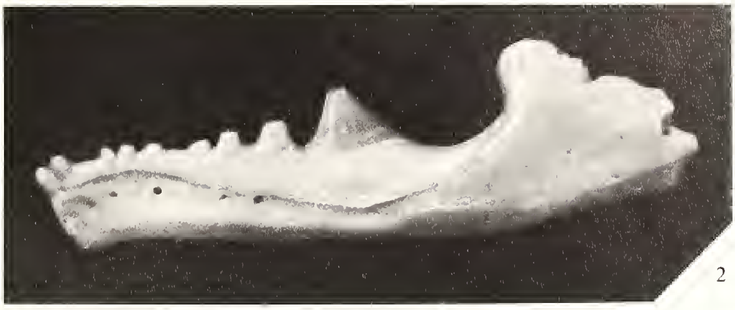

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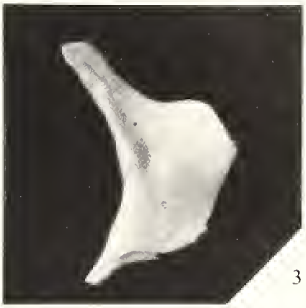

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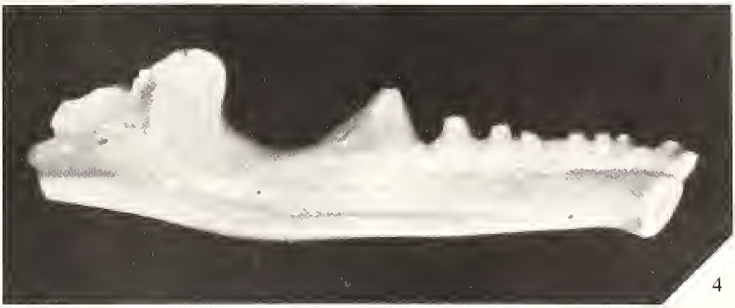

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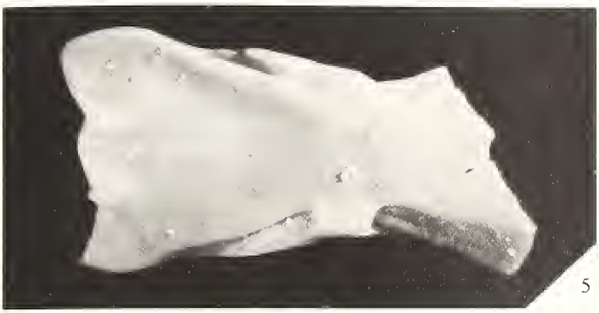

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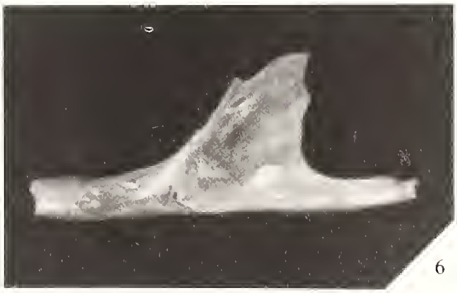

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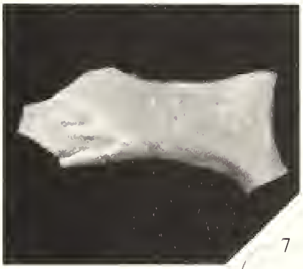

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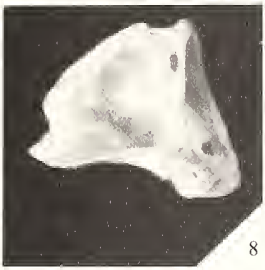

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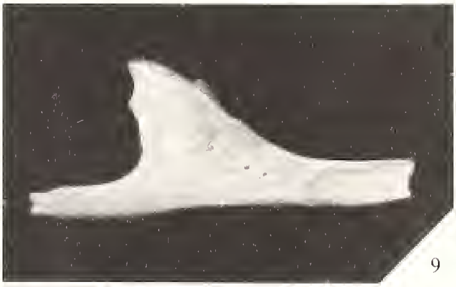

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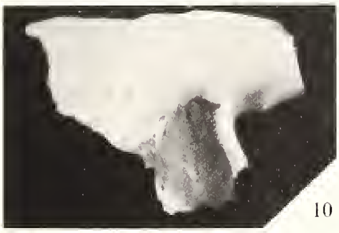

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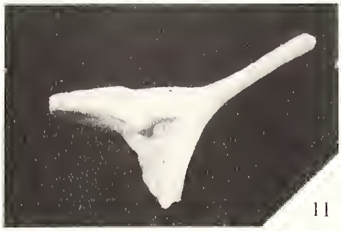

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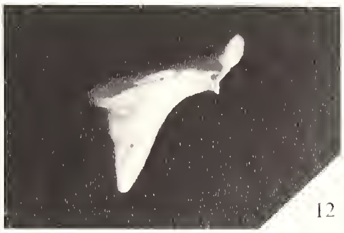

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FRASER, *Planocephalosaurus*

Description. Dermal bones of the skull roof. The premaxillae extend a short distance ventrally to form a rudimentary beak. They separate the external nares and meet medially in long narrow vertical processes that extend into slot facets between the nasals. Below the external naris a posterior extension of the premaxilla is slightly overlapped by the maxilla and this fairly weak contact may have been strengthened by ligaments. Four teeth are characteristically present (Pl. 70, fig. 1), but they remained discrete throughout life and, unlike *Clevosaurus* and *Sphenodon*, did not tend to become worn into a single chisel-like structure in more mature individuals. Posterior to the teeth is a short palatal shelf.

The maxillae (Pl. 69, figs. 1 and 3) extend the full depth of the external nares defining the lower anterior quadrant of each orbit. They strongly overlap both the nasals and the prefrontals at their upper limits, thereby bracing the snout. Approximately two-thirds of the ventral border of either orbit is formed by the maxilla, and the jugal contact slopes posteroventrally from this border. Mesially there is a large foramen (Pl. 69, fig. 3) which was continuous with a similar foramen in the palatine contact and this carried the maxillary nerve and artery. The lateral surfaces of the maxillae are perforated by a series of small foramina which carried the nerves and blood vessels that supplied the skin. Usually each maxillae bears twelve to fourteen acrodont teeth, rarely up to seventeen. Four basic tooth categories can be recognized: the anterior three or four teeth are approximately 1·0 mm high, conical, and with a slightly recurved apex. These are followed posteriorly by a variable number of smaller conical teeth, usually three but up to seven, which in rare instances exhibit a slight alternation in size. These teeth never exceed 0·6 mm. The succeeding four teeth increase in size from about 0·6 mm anteriorly to over 1·0 mm in the most posterior member of the series. They are obtusely conical with broad bases and each bears a small posterolingual flange. The flange is comparable with those of *Sphenodon* and *Clevosaurus*, but less well developed. Three obtusely conical teeth approximately 0·5 mm high occur posterior to the flanged series. All teeth bear a distinct radial ribbing that is most prominent on the lingual surfaces (Pl. 69, figs. 2 and 4).

Anteriorly the paired nasals (Pl. 70, fig. 10) narrow to slender processes that descend ventrally and embrace the premaxillae. At their posterior limits there are transverse sutures with the frontal. The nasals descend partly over the sides of the skull and broad depressions receive the anterodorsal edges of the maxillae, so that jointly the maxillae and nasals form the posterior boundary of the external nares. The nasals also bear facets for the prefrontals.

The prefrontals overlap the nasals and form the anterodorsal quadrant of each orbit. At their posterior limits they extend to a point nearly mid-way along the supraorbital margin where there is a distinct interlocking of prefrontal with frontal (text-fig. 2*b*). A medial flange of the prefrontal descends along the anterior border of the orbit to articulate in a complex socket on the dorsal surface of the palatine (Pl. 71, fig. 4).

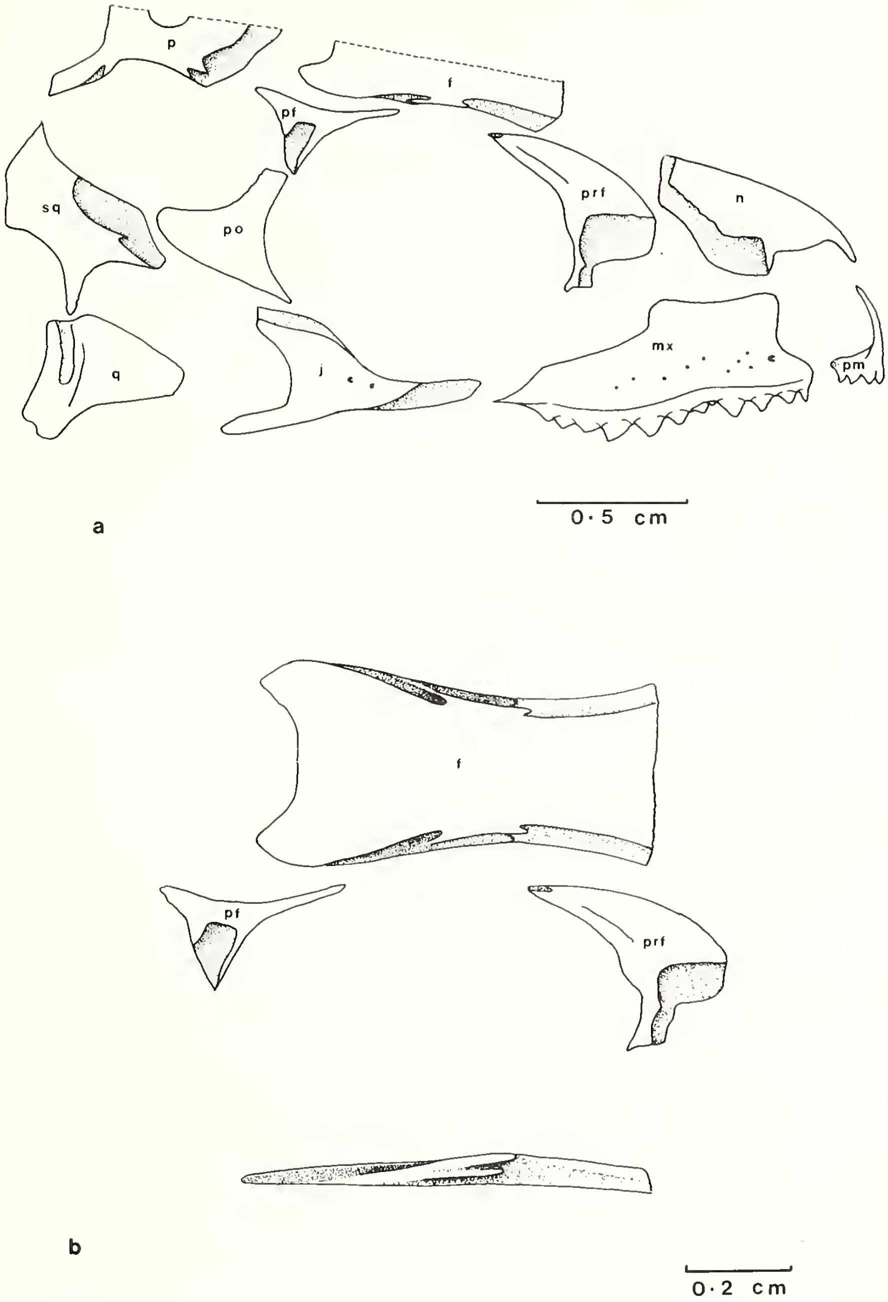
No lacrimals have been recognized and there are no facets on the prefrontals which might suggest their presence.

The frontal is a single element (Pl. 70, fig. 5) with transverse sutures separating it anteriorly from the nasals and posteriorly from the parietals. It forms the supraorbital margin for a short distance between the prefrontals and postfrontals and has rigid contacts with these elements (text-fig. 2*b*).

The parietals are fused, unlike the primitive situation, and form a broad and flat skull roof which is perforated by a well-developed parietal foramen. Anteriorly there are facets to receive the postfrontals and frontal (Pl. 70, fig. 7), and posteriorly lateral processes meet the squamosals.

Essentially triradiate bones, both postfrontals possess a long slender anterior process that slots into a narrow groove situated on the posterolateral margin of the frontal, and a shorter posterior process that articulates with the anterolateral edge of the parietal (Pl. 70, fig. 11). The third process is ventrolaterally directed and bears a depression to receive the postorbital; combined, these two elements jointly form the posterior border of the orbit. The postfrontals also enter into the anterior margins of the upper temporal fossae.

The postorbitals (Pl. 70, fig. 3) are approximately triangular bones that strongly overlap the squamosals posteriorly, and descend ventrally to meet and slightly overlap the jugals. A large area of contact between the postorbital and postfrontal is responsible for a rigid postorbital bar. There is no contact between the postorbital and the parietal.



TEXT-FIG. 2. *a*, The membrane bones of the skull indicating individual facets for articulation with adjacent elements. *b*, Detailed reconstruction of the articulation facets of the frontal, prefrontal, and postfrontal in dorsal view and the frontal in right lateral view.

Abbreviations used in figures. f = frontal; j = jugal; mx = maxilla; n = nasal; p = parietal; pf = postfrontal; pm = premaxilla; po = postorbital; prf = prefrontal; q = quadrate; sq = squamosal.

The maxillae overlap the anterior process of each jugal so that a combination of maxilla and jugal forms much of the ventral margin of each orbit. Posterior to the orbit the jugal slightly overlaps the anterior edge of the squamosal and thereby excludes the postorbital from the margin of the lower temporal fossa. A slender process extends posteriorly towards the quadratojugal and in the majority of specimens examined, including adults as well as juveniles, it tapers away to a rounded point so that the lower temporal bar is incomplete. However, of the fifty-one jugal specimens so far recovered, one exhibits notches at the posterior limit of this process that suggests an articulation with the quadratojugal and squamosal as reconstructed in text-fig. 3*b*. It would therefore appear that in one or two individuals at least the lower temporal bar was complete. The palatal borders of the jugals display raised facets for articulation with the ectopterygoids (Pl. 70, fig. 6).

The squamosals form the posterior region of the upper temporal arcades, extending anteriorly underneath the postorbitals and the jugals. All three bones contribute to the separation of the upper and lower temporal fossae. Posteromesially the squamosal narrows into a slender inwardly directed process that fits into a narrow slot on the lateral process of the parietal. There are no supratemporals and together the parietal and squamosals form the posterior margins of the upper temporal fenestrae. The ventral ramus of the squamosal is continuous with the lateral edge of the quadratojugal and may have provided a framework for a tympanic membrane. In most specimens this ventral ramus only extended part-way down the quadratojugal before tapering away, but in one specimen this ramus continues the full length of the quadratojugal and at the ventral extremity expands anteriorly to make a weak contact with the jugal (Pl. 71, fig. 8). This confirms the observation of the jugal specimen, which suggested that some individuals of *Planocephalosaurus* possessed a complete lower temporal bar with a weak articulation between jugal, quadratojugal, and squamosal. But more generally it seems likely that full ossification in this region did no occur in the embryo, thereby leaving a small gap in the lower temporal bar. The dorsal head of the quadrate was supported by a flange that extends mesially between the quadratojugal process and the posterolateral corner of the squamosal.

The quadrate and quadratojugal are fused with no visible sutures (Pl. 70, fig. 8). Generally this element has not been well preserved in the bone assemblages, particularly with respect to the quadratojugal region, and there is little evidence of the facet that articulates with the ventral ramus of the squamosal. The quadrate was clearly rigidly attached to the squamosal and the pterygoid, since its dorsal head was supported by a flange on the squamosal and a well-developed anteromesially directed lamina of bone broadly overlapped a posterolateral flange of the pterygoid. A lateral conch provided the support for a tympanic membrane.

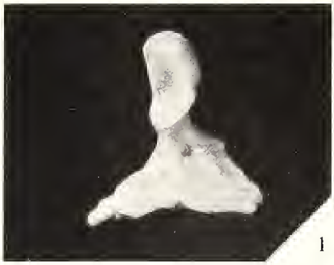
The palate. The vomers extend from the premaxillae to the pterygoids, articulating with the latter bones by means of interlocking flanges. At their posterolateral edges they overlap the palatines and laterally they bound the internal nares. Small teeth are scattered across much of the ventral surface, but one or sometimes two teeth lying immediately posterior to the premaxillae and adjacent to the vomerine aperture are usually a little larger and more prominent than the rest.

The palatines extend from the posterior border of the internal nares to a point almost adjacent to the posterior limits of the maxillae, with which there are restricted contacts. Mesially they are bounded by the pterygoids and are thereby excluded from the interpterygoid vacuity. On the dorsal surface there is an anterior facet for the prefrontal (Pl. 71, fig. 4). On the ventral surface of the

EXPLANATION OF PLATE 71

Fig. 1. An epipterygoid specimen, AUP No. 11075, considered to be *Planocephalosaurus robinsonae* gen. et sp. nov., × 10.

Figs. 2–9. *P. robinsonae* gen. et sp. nov. 2, a parabasisphenoid, AUP No. 11076, in ventral view, × 5. 3, ventral view of a basioccipital, AUP No. 11077, × 5. 4, dorsal view of a left palatine, AUP No. 11078, × 10. 5, ventral view of a left palatine, AUP No. 11078, × 10. 6, lateral aspect of a left squamosal, AUP No. 11079, × 10. 7, dorsal view of a left pterygoid, AUP No. 11080, × 10. 8, lateral aspect of the single squamosal specimen, AUP No. 11081, possessing a jugal contact, × 10. 9, a left pterygoid, AUP No. 11080, in ventral view, × 10.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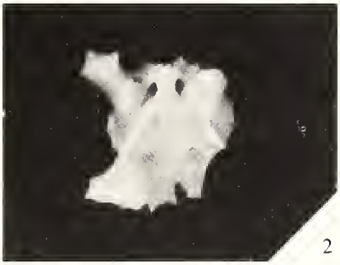
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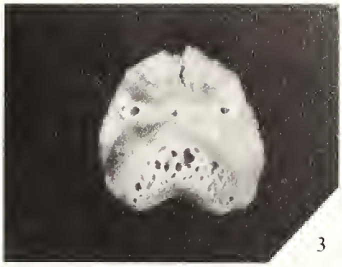
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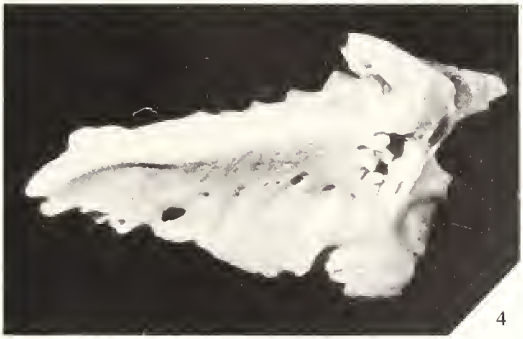
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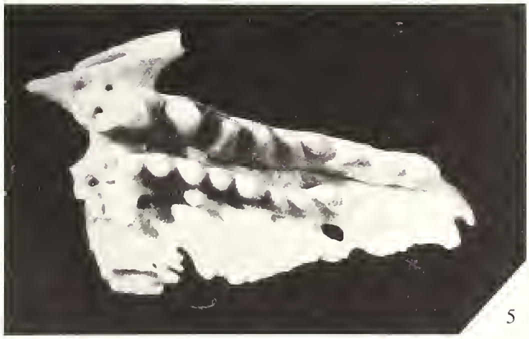
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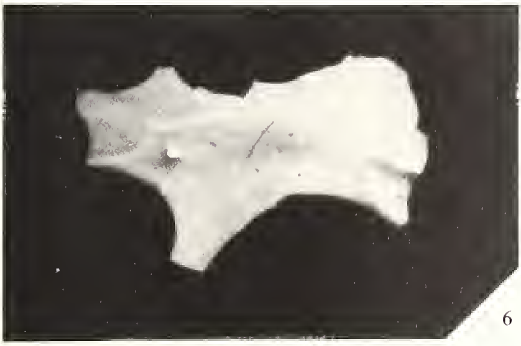
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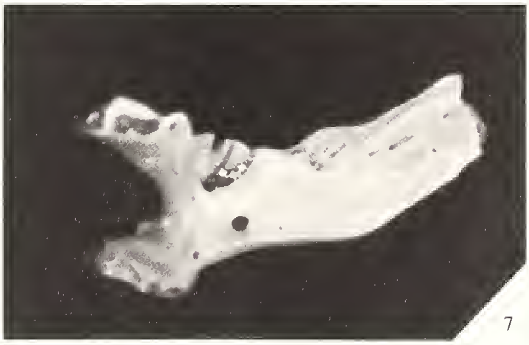
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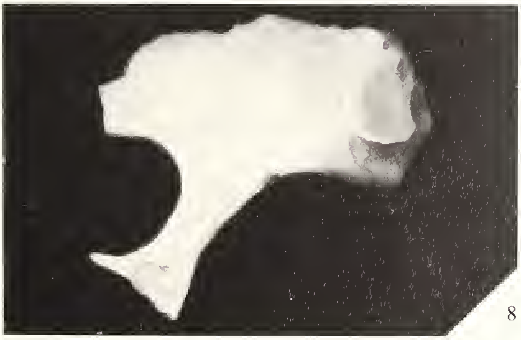
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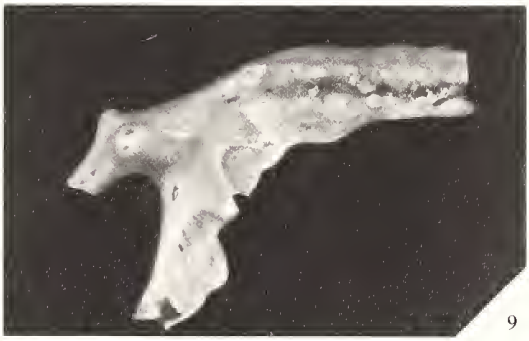
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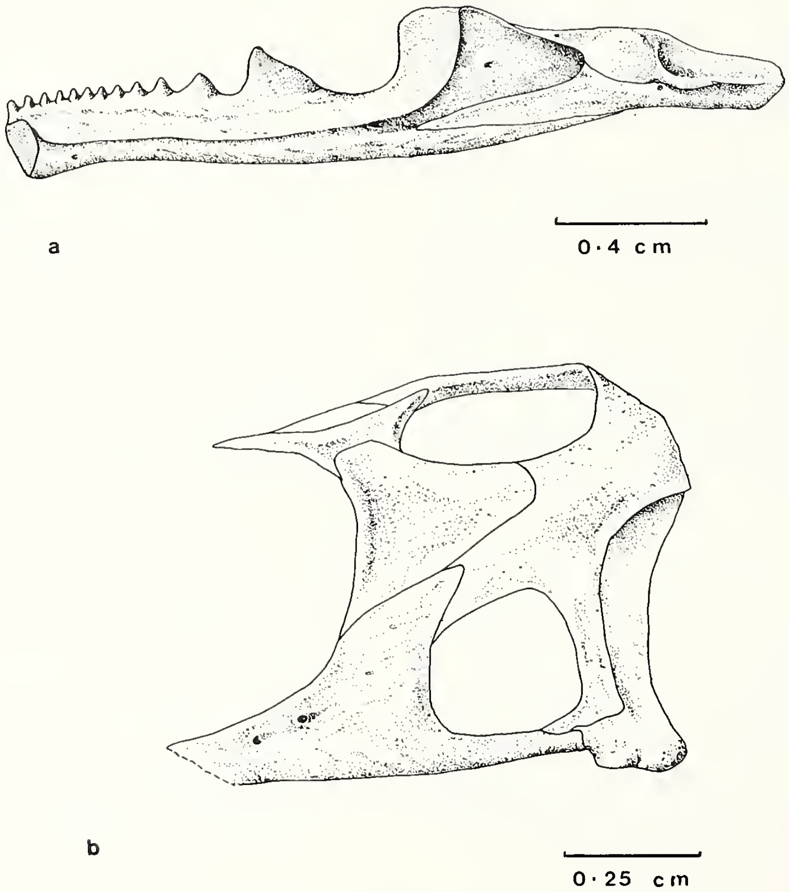
FRASER, *Planocephalosaurus*

palatines there are characteristically two tooth-rows, which anteriorly run parallel to the marginal dentition but diverge somewhat mesially in the posterior part of the element (Pl. 71, fig. 5). Additional teeth may form a third row. The most lateral tooth-row typically bears ten teeth; the anterior four or five being similar to the maxillary teeth to which they lie adjacent, and displaying labial facets reflecting wear through shearing movements. The remaining five or six teeth in this row are smaller and do not exhibit such labial facets. The second row usually consists of twelve to fourteen uniform teeth similar to the posterior teeth of the most lateral row. A rudimentary third row is normally marked by only two anterior teeth, but up to six may be present. All palatal teeth are marked by the radial ribbing pattern characteristic of the marginal dentition.

Anteriorly the pterygoids meet along the midline by means of interdigitating facets, but more posteriorly they diverge to form a narrow interpterygoid vacuity. As described above the pterygoids reach forward to the vomers and lateral facets on their dorsal surfaces provide broad contacts with the palatines (Pl. 71, fig. 7). The palatal ramus of each pterygoid bears a number of radially ribbed teeth that are roughly arranged into two rows (Pl. 71, fig. 9), although in some specimens there is also



TEXT-FIG. 3. *Planocephalosaurus robinsonae* gen. et sp. nov. *a*, Reconstruction of the dentary and articular complex in lingual view, and *b*, an alternative structure of the temporal region of the skull where the lower temporal bar is complete.

evidence of a third row situated just anterior to the pterygoid flange. The quadrate process is a deep, mesially concave flange that passes posterolaterally and broadly overlaps a similar-shaped process on the quadrate. The basipterygoid process of the parabasisphenoid articulates in a mesial depression situated anterior to the quadrate ramus, and on the ventral surface immediately anterior to this depression there is a small protuberance. Laterally the pterygoids have broad contacts with the ectopterygoids and together they form a deep pterygoid flange to guide the action of the lower jaw.

Laterally the ectopterygoids are expanded anteroposteriorly and there is a notch facet on this surface for the jugal. Passing posteromesially the ectopterygoids expand dorsoventrally to the contacts with the pterygoids.

Thirteen '*Sphenodon*-like' epipterygoids provisionally attributed to *Planocephalosaurus* have been recovered (Pl. 71, fig. 1). However, the pterygoid and quadrate specimens of *Planocephalosaurus* that have been recorded do not bear detailed epipterygoid articulation facets, so that some doubt remains regarding the origin of the epipterygoids; nevertheless, their abundance and size indicates that they are representatives of *Planocephalosaurus*. They have an expanded ventral head which presumably articulated with the quadrate and pterygoid. The shaft is expanded dorsally and fibrous tissue probably attached it to the parietal and supraoccipital.

The braincase. The braincase is not as well represented in the assemblages as the skull roof elements, and only the parabasisphenoid, basioccipital, and exoccipitals are present in sufficient numbers and with sufficient detail to make any comment. Different hydrodynamic properties may partly account for this poor representation of the braincase, but, because of the greater complexity of the braincase, fragmentary specimens are also more difficult to interpret than those from the skull roof.

The parasphenoid has become fused to the ventral surface of the basisphenoid to form a single unit, the parabasisphenoid (Pl. 71, fig. 2). Posteriorly the parabasisphenoid has a broad overlapping contact with the basioccipital, and laterally there are facets for the prootic bones. The basipterygoid processes arise laterally to the carotid foramina and, diverging slightly, extend forward into sockets in the pterygoids. Anteriorly the lateral margins of the parabasisphenoid converge to form a narrow cultriform process that extends an unknown distance into the interpterygoid vacuity.

Exoccipitals are occasionally recovered fused to the basioccipital, but usually they are separate as a result of the disintegration of the narrow exoccipitals, which are extremely vulnerable and fragile. A well-marked facet on the anterior ventral surface of the basioccipital receives the parabasisphenoid, and a pair of well-developed basal tubera situated more posteriorly (Pl. 71, fig. 3) were for the attachment of neck muscles. The occipital condyle forms the posterior limit of the basioccipital.

The exoccipitals are slender columnar structures fused to the posterior dorsal surface of the basioccipital, forming the lateral margins of the occipital condyle. They are pierced by foramina that accommodated branches of the hypoglossal nerve. Their facets for the opisthotics are unknown.

The lower jaw. Only two elements have been identified from the lower jaw, the dentary and an articular complex. The articular complex is considered to be a fusion of the articular with the overlying dermal elements: the prearticular, angular, and surangular. Neither splenial nor coronoid bones have been identified.

The dentaries meet anteriorly at the jaw symphysis and extend posteriorly to the articular complex. Posterior to the tooth ramus the dentaries expand dorsoventrally to form at least part of the coronoid process, extending slightly higher than the most posterior tooth. Mesially there is thought to have been no splenial and the Meckelian canal apparently remained open. Normally there are thirteen or fourteen radially ribbed teeth, of which the anterior eight or nine are generally of a uniform size, approximately 0·4–0·6 mm high. The four or five remaining teeth progressively increase in size posteriorly and the last often exceeds 2·0 mm. This most posterior tooth is characteristic and bears a rudimentary anterolabial flange. In labial view it has a relatively elongate base and marked anteroposterior asymmetry; the anterior edge is slightly concave, but owing to a slight shoulder the posterior edge is convex. All teeth are laterally compressed, but less so in anterior members. Only the posterior tooth bears a flange of any description.

Since no sutures define the limits of the articular, prearticular, angular, and surangular, this group of elements is best described as a single unit. The most prominent features are the glenoid fossa, which receives the condyles of the quadrate, and, anterior to this fossa, the adductor fossa. The lateral surface of the complex bears a large facet for the posterior ramus of the dentary, which provided a rigid bond between the two major elements of the lower jaw.

Postcranial elements. The bone assemblages contain a number of dissociated postcranial elements that include abundant pelvic and pectoral girdle fragments, vertebrae, ribs, epipodials, propodials, and phalanges. They represent a reptile of similar size to the new species and bear many sphenodontid characters. It is hoped that these specimens will be used in future work to make a full reconstruction of the postcranial skeleton of *Planocephalosaurus*.

DISCUSSION

Certain features of *Planocephalosaurus*, in particular the temporal region and the roof of the skull, raise important questions concerning the classification of some of the smaller diapsids. The first modern attempt to organize the taxonomy of these diapsids was by Romer (1966), who classified the eosuchians, squamates, and rhynchocephalians as separate orders within the subclass Lepidosauria, and considered the subclasses Archosauria and Lepidosauria as having separate ancestries (Appendix 2). Kuhn (1969) modified the subclass Lepidosauria to include the orders Rhynchocephalia, Squamata, and Protorosauria. As he defined the order Rhynchocephalia it incorporated eight suborders including the Eosuchoidea, Rhynchosauroidea, and Sphenodontoidea. The order Protorosauria incorporated four suborders, and these included the Protorosauroidea, Prolacertoidea, and the Tanysitracheloidea (Appendix 2). Like Romer, Kuhn believed the Kuehneosauridae to be true lacertilians.

More recently the eosuchians have been accredited with rather more significance than an assorted assemblage of primitive diapsid genera since Cruickshank (1972) and Carroll (1976) argue the case for the eosuchians as the ancestors to both the Squamata and Archosauria as well as other diapsids. Taking this latter viewpoint, the taxonomic position of the rhynchocephalians, including the Sphenodontidae, is called into question.

In a further review of diapsid classification Evans (1980) recognizes a subclass Diapsida within which there are three infraclasses; the first is the Eosuchia, which gave rise to the remaining two; the Archosauria and the Squamata. The term Lepidosauria becomes redundant, and as she defines the Eosuchia it contains sixteen families, including the Sphenodontidae and the rest of the rhynchocephalians (Appendix 2).

Planocephalosaurus possesses a number of features in common with *Sphenodon*, *Clevosaurus*, *Homeosaurus*, and others, including acrodont dentition, pterygoids reaching forward to the vomers, and absence of the tabulars, postparietals, and lacrimals. These characteristics clearly indicate that the genus belongs to the family Sphenodontidae. However, it also shares a number of characteristics with the eosuchians and some lizards, and is therefore important in considering the taxonomic position of the Sphenodontidae.

Perhaps the most advanced feature of *Planocephalosaurus* is the presence of fused frontals and parietals, a characteristic shared by *Gephyrosaurus* and lizards, but not seen in either *Clevosaurus* or *Sphenodon*. An essentially primitive feature, however, is the retention of a large central parietal foramen shared with *Youngina*, *Tanystropheus*, *Gephyrosaurus*, *Clevosaurus*, and others. Thus, with respect to the skull roof *Planocephalosaurus* exhibits both primitive and advanced characteristics and is very similar to *Gephyrosaurus*.

The absence of a lacrimal in *Planocephalosaurus* is a characteristic shared by *Sphenodon*, but many eosuchians, including *Gephyrosaurus*, *Youngina*, and *Tanystropheus*, retain a lacrimal. However, with respect to other features of the circumorbital elements, *Planocephalosaurus* is similar to *Gephyrosaurus*, *Youngina*, and *Tanystropheus* as well as *Sphenodon* and *Clevosaurus*. All these species possess a triradiate postfrontal that enters the border of the upper temporal fenestra, and this is in contrast to

Icarosaurus, *Kuehneosaurus*, and *Prolacerta*. In *Gephyrosaurus* and *Clevosaurus* the postorbital is excluded from the boundary of the lower temporal fenestra by the apposition of the jugal and squamosal; this is also the condition observed in *Planocephalosaurus*.

No supratemporal bone is present in *Planocephalosaurus*, *Sphenodon*, or *Gephyrosaurus*, but *Clevosaurus* retains this element. However, all four genera possess a similar squamosal with a ventral ramus attached firmly to the quadratojugal and the squamosal forming the sole support for the head of the quadrate. These four genera also have a deep overlap between pterygoid and quadrate, which would have inhibited any streptostylic movement.

The arrangement of the acrodont teeth in *Planocephalosaurus* is similar to *Sphenodon* and *Clevosaurus*, with the largest biting teeth occurring at the back of the jaw ramus and the possession of enlarged palatine tooth rows. In *Sphenodon* the articular surface for the quadrate is elongated, thereby allowing for antero-posterior movement at this articulation, and, as Robinson (1976) has shown, the wear facets on the lateral surface of the dentary show that propalinal movement occurs whilst feeding. Evans (1980) postulated that *Gephyrosaurus* may have had a similar feeding action to *Sphenodon*, as it too has an elongated articular surface on the lower jaw. There is also an enlarged tooth row on the palatine of *Gephyrosaurus*, and Evans believes that propalinal feeding movements best explain this character. However, *Clevosaurus* also bears an enlarged palatine tooth-row and, as Robinson (1976) states, in this species there was a precise occlusion of the teeth, as indicated by the impression of the individual maxillary teeth that have been scored on the dentary; therefore no propalinal movement of the jaw was involved in the feeding action. Thus, the enlarged palatine tooth-row is not necessarily a feature solely associated with propalinal jaw movements, but may have aided with the grasping and crushing of relatively large prey.

In *Planocephalosaurus* the articular surface for the quadrate is somewhat elongated and there are faint scoring marks on the lateral surface of the dentary, which suggest that small propalinal movements occurred, but not to the same extent as *Sphenodon*. Individual maxillary tooth impressions are still recognizable on the *Planocephalosaurus* dentary (Pl. 69, fig. 6), but these are not as precisely defined as those of *Clevosaurus*.

Like *Gephyrosaurus*, the snout region of *Planocephalosaurus* is well braced, with firm contacts between the nasals, prefrontals, maxillae, and palatines that would resist pressures resulting from feeding on relatively difficult material, and as Evans (1980) indicates the single frontal and parietal may be regarded as a further adaption in the general strengthening of the skull.

The reduction of the lower temporal bar in such forms as *Kuehneosaurus*, *Icarosaurus*, and *Prolacerta* has been accepted in the past as an essentially squamate or ‘presquamate’ character. In some instances the lower temporal bar is complete in *Planocephalosaurus* (text-fig. 3*b*), but generally it is very similar to *Clevosaurus* and *Gephyrosaurus* in this respect and is incomplete. This gap in the lower temporal bar is therefore no longer acceptable as a uniquely squamate or ‘presquamate’ condition, and reasons other than streptostyly must be looked for to account for the appearance of this character in a variety of genera. Although Robinson (1973) suggested that in *Clevosaurus* this feature might improve the reception of airborne sound, it would seem unlikely to be effective in completely isolating the tympanic membrane from feeding sounds transmitted from the dentition, and, as Evans (1980) proposed, it was more likely to have occurred as a result of a change in the action and arrangement of the jaw adductor musculature.

Haas (1973) reports that in *Sphenodon* the origins of the adductor mandibulae muscle complex are variable. Very little of this complex is actually attached to the lower temporal bar, with the exception of the M. Levator anguli oris, which in some instances has been found to originate from the medial surface of the quadratojugal ramus of the jugal, while in others it may originate as high as the anteromedial surface of the postorbital. The M. Levator anguli oris is also present in lizards, but as a result of the loss of the lower temporal bar, the origins of the muscle have moved entirely to the upper temporal arch. If for some reason it became advantageous for a diapsid with both temporal bars complete to have a longer M. Levator anguli oris then its origin might move to a higher position on the upper temporal arch, and consequently the lower temporal bar would be made completely redundant for muscle attachment and might therefore fail to ossify fully. In lizards the loss of the lower temporal bar is associated with the highly kinetic skull, but this is not an explanation for the atrophy observed in the lower temporal bar of *Planocephalosaurus*, since in this species the pterygoid and quadrate are firmly attached and kinesis is restricted. If in *Planocephalosaurus* the M. Levator anguli oris originated exclusively on the postorbital, then a reduction in ossification of the lower temporal bar might be expected. The consequent increase in length of the M. Levator anguli oris may have been coupled with an increase in length of other adductor muscles, a change which could result in greater speed of adduction. This might be of value in facilitating quick snapping movements of the jaws when taking small insects. *Planocephalosaurus* is considered likely to have had a very varied diet, having been equipped with large shearing teeth at the posterior end of the jaw, enabling large insects with resistant cuticles and maybe the occasional small vertebrate to be masticated, while the sharper more pointed teeth on the premaxilla and anterior regions of the maxilla and dentary would have been capable of snapping and impaling smaller insects and grubs. Both the speed of contraction and the force of contraction of the jaw adductor musculature may well have been important in such a varied diet.

Whilst *Planocephalosaurus* closely resembles *Gephyrosaurus* in the structure of the skull roof and the temporal region, the acrodont implantation of the dentition contrasts markedly with the pleurodont insertion displayed by *Gephyrosaurus*. Similarly, *Planocephalosaurus* has close affinities with *Clevosaurus* and *Sphenodon*, and these three genera are considered to be members of the family Sphenodontidae. The affinities of *Planocephalosaurus* and *Gephyrosaurus* are probably due to the relationship of the two families Gephyrosauridae and Sphenodontidae; both are included within the infraclass Eosuchia as outlined by Evans (1980).

Appendix 2 illustrates three different classifications of some diapsid reptiles, and it is clearly seen how confusion has arisen regarding the systematics of many diapsid genera; often this has resulted in the different usage of similar terms. The current belief that *Petrolacosaurus* is an early Carboniferous diapsid (Reisz 1977) lends support to the Evans classification with an infraclass Eosuchia giving rise to the Archosauria and Squamata, but the arrangement of orders within the Eosuchia remains a problem. In Romer's (1966) classification those diapsids with an acrodont dentition, but which in other respects may be quite different, have unfortunately been grouped together in one order, the Rhynchocephalia. Kuhn (1969) partly solved this problem by favouring the use of a number of suborders within each order, but his use of the term Rhynchocephalia is rather misleading in that it includes the suborder Eosuchoidea. Whilst Evans (1980) does not arrange the families of the infraclass Eosuchia either into orders or suborders, she admits that an order Rhynchocephalia may be useful, and I propose that such an order could be structured as in Table 1, consisting of forms derived from the eosuchians of the Permian and Lower Triassic (Hoffstetter 1955). The four suborders are all characterized by an acrodont dentition, or are toothless and evidently derived from the acrodont condition.

The Sphenodontoidea is a clearly characteristic suborder incorporating the only living genus, *Sphenodon*. Diagnostic features of the family Sphenodontidae include a diapsid skull, acrodont dentition, pterygoids elongated anteriorly to meet the vomers, an immobile quadrate firmly overlapping the pterygoid, amphicoelous vertebrae, 23–25 presacral vertebrae, 2 sacral vertebrae, and autotomy septa present in the caudal vertebrae. *Monjurosuchus* was classified as a member of the

TABLE 1. Classification of the order Rhynchocephalia

Infraclass	Order	Suborder	Family	
Eosuchia	Rhynchocephalia	Sphenodontoidea	Monjurosuchidae	e.g. *Monjurosuchus*
			Sphenodontidae	e.g. *Sphenodon*, *Clevosaurus*
		Sapheosauroidea	Sapheosauridae	e.g. *Sapheosaurus*
		Rhynchosauroidae	Mesosuchidae	e.g. *Mesosuchus*
			Rhynchosauridae	e.g. *Rhynchosaurus Scaphonyx*
		Clarazisauroidea	Claraziidae	e.g. *Clarazia*

family Sphenodontidae by Romer (1966), but differences, including the presence of 3 sacral vertebrae, indicate a separation from the Sphenodontidae and, following Hoffstetter (1955) and Kuhn (1969), *Monjurosuchus* is assigned to a separate family, the Monjurosuchidae.

The skull structure of the Rhynchosauroidea is easily derived from that of the Sphenodontoidea with modifications associated with the specialized herbivorous diet. The suborder can be separated into two families. The Mesosuchidae, which are similar to the Sphenodontoidea in bearing teeth on the premaxilla and in having the parietal pierced by a pineal foramen, have acquired the single median nasal opening and the rudiments of lateral tooth-rows on the maxilla, so characteristic of the Rhynchosauridae. The Rhynchosauridae are heavily built forms with large and complex tooth batteries on the maxilla and dentary and a toothless premaxilla.

The two remaining suborders, the Sapheosauroidea and Clarazisauroidea, are not as well documented, much of the fossil material being fragmented and poorly preserved. The postcranial skeleton of the Sapheosauroidea is similar to that of *Homeosaurus* (Hoffstetter 1955, Romer 1956). The Clarazisauroidea was erected by Peyer (1936*a*, *b*) for two genera of aquatic reptiles—both with an acrodont dentition, an immobile quadrate, and amphicoelous vertebrae.

Pleurosaurus is a rather aberrant acrodont genus that was classified by Romer (1966) as a rhynchocephalian. However, it has an unusual temporal region that is euryapsid in nature, and Hoffstetter (1955), while recognizing some affinities to the rhynchocephalians, considers the differences to be sufficiently great to merit a separate order, the Pleurosauria; and this classification is followed here.

The Sphenodontoidea may include the family erected by Kuhn (1969) to incorporate the Lower Triassic acrodont genus *Palacrodon*. But, as Malan (1963) points out, this genus might just as easily be considered to be an aberrant procolophonid or lizard as an aberrant rhynchocephalian. Hoffstetter (1955) postulates that it may be a remote ancestor of the Pleurosauria or possibly at the evolutionary point of separation of the Rhynchocephalia and Pleurosauria. There is insufficient evidence to permit the inclusion of *Palacrodon* in the Rhynchocephalia and its position remains uncertain.

Because of insufficient evidence at present, the remaining Eosuchian families listed by Evans (1980) have not been assembled into larger units.

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APPENDIX 1

Total numbers of each skull element recovered from Cromhall Quarry

Element	pm	mx	n	prf	f	p	pf	po	j	sq	q	v	pal	pt	ps	bo	d
Number of *Planocephalosaurus* elements from a single site and stratum	19	61	18	21	27	17	17	18	36	8	7	5	42	18	6	6	99
Number of *Planocephalosaurus* elements recovered in total	46	115	32	30	36	27	33	28	51	24	18	17	93	49	19	23	146
Total number of elements of all species represented in the bone assemblages	61	161	37	32	45	30	51	36	69	33	18	17	112	50	19	23	232

Abbreviations	bo	basioccipital	p	parietal	ps	parabasisphenoid
	d	dentary	pal	palatine	pt	pterygoid
	f	frontal	pf	postfrontal	q	quadrate
	j	jugal	pm	premaxilla	sq	squamosal
	mx	maxilla	po	postorbital	v	vomer
	n	nasal	prf	prefrontal		

APPENDIX 2 *Three alternative classifications of the diapsid reptiles excluding details of the lizards and archosaurs*

	Subclass	Infraclass	Order	Suborder	Family	
ROMER (1966)	EURYAPSIDA		ARAEOSCELIDA		TANYSTROPHEIDAE	e.g. *Tanystropheus*
					PROTOROSAURIDAE and others	e.g. *Protorosaurus*, *Trachelosaurus*
	LEPIDOSAURIA		EOSUCHIA		YOUNGINIDAE	e.g. *Palaeogama*, *Paliguana*, *Youngina*
					TANGASAURIDAE	e.g. *Tangasaurus*
					CHAMPSOSAURIDAE	e.g. *Champsosaurus*
					THALATTOSAURIDAE	e.g. *Thalattosaurus*, *Askeptosaurus*
					PROLACERTIDAE	e.g. *Macronemus*, *Prolacerta*
			SQUAMATA		KUEHNEOSAURIDAE and others	e.g. *Kuehneosaurus*, *Icarosaurus*
			RHYNCHOCEPHALIA		SPHENODONTIDAE	e.g. *Clevosaurus*, *Homeosaurus*, *Sphenodon*
					RHYNCHOSAURIDAE	e.g. *Howesia*, *Mesosuchus*, *Scaphonyx*
					SAPHEOSAURIDAE	e.g. *Sapheosaurus*
					CLARAZIIDAE	e.g. *Clarazia*
					PLEUROSAURIDAE	e.g. *Pleurosaurus*
	ARCHOSAURIA					
KUHN (1969)	ARAEOSCELOMORPHA		ARAEOSCELIDA		PETROLACOSAURIDAE and others	e.g. *Petrolacosaurus*
	LEPIDOSAURIA		RHYNCHOCEPHALIA	EOSUCHOIDEA	YOUNGINIDAE	e.g. *Youngina*
					PALIGUANIDAE	e.g. *Paliguana*, *Palaeagama*
					TANGASAURIDAE	e.g. *Tangasaurus*
				SPHENODONTOIDEA	POLYSPHENODONTIDAE	e.g. *Polysphenodon*
					SPHENODONTIDAE	e.g. *Clevosaurus*, *Homeosaurus*, *Sphenodon*
				SAPHEOSAUROIDEA	SAPHEOSAURIDAE	e.g. *Sapheosaurus*
				PLEUROSAUROIDEA	PLEUROSAURIDAE	e.g. *Pleurosaurus*
				RHYNCHOSAUROIDEA	MESOSUCHIDAE	e.g. *Mesosuchus*
					RHYNCHOSAURIDAE	e.g. *Howesia*, *Rhynchosaurus*, *Scaphonyx*
				CLARAZISAUROIDEA	CLARASIIDAE	e.g. *Clarazia*
				THALATTOSAURDIDAE	THALATTOSAURIDAE	e.g. *Thalattosaurus*
					ASKEPTOSAURIDAE	e.g. *Askeptosaurus*
				CHORISTODEROIDEA	CHAMPSOSAURIDAE	e.g. *Champsosaurus*
			PROTOROSAURIA	PROTOROSAUROIDEA	PROTOROSAURIDAE	e.g. *Protorosaurus*
				PROLACERTOIDEA	PROLACERTIDAE	e.g. *Prolacerta*, *Macronemus*
				TANYSITRACHELOIDEA	TANYSTROPHEIDAE	e.g. *Tanystropheus*
			SQUAMATA		KUEHNEOSAURIDAE and others	e.g. *Kuehneosaurus*, *Icarosaurus*
	ARCHOSAURIA					
EVANS (1980)	DIAPSIDA	EOSUCHIA			PETROLACOSAURIDAE	e.g. *Petrolacosaurus*
					YOUNGINIDAE	e.g. *Youngina*
					TANGASAURIDAE	e.g. *Tangasaurus*
					ASKEPTOSAURIDAE	e.g. *Askeptosaurus*
					THALATTOSAURIDAE	e.g. *Thalattosaurus*
					PLEUROSAURIDAE	e.g. *Pleurosaurus*
					SPHENODONTIDAE	e.g. *Clevosaurus*, *Homeosaurus*, *Sphenodon*
					MESOSUCHIDAE	e.g. *Mesosuchus*
					RHYNCHOSAURIDAE	e.g. *Rhynchosaurus*, *Scaphonyx*
					CLARAZIIDAE	e.g. *Clarazia*
					DAEDALOSAURIDAE	e.g. *Daedalosaurus*
					PALIGUANIDAE	e.g. *Paliguana*, *Palaeagama*
					TANYSTROPHEIDAE	e.g. *Tanystropheus*
					PROLACERTIDAE	e.g. *Prolacerta*, *Macronemus*, ?*Protorosaurus*
					KUEHNEOSAURIDAE	e.g. *Kuehneosaurus*, *Icarosaurus*
					GEPHYROSAURIDAE	e.g. *Gephyrosaurus*
		SQUAMATA				
		ARCHOSAURIA				

BUCHIID BIVALVES FROM THE UPPER JURASSIC AND LOWER CRETACEOUS OF EAST GREENLAND

by F. SURLYK *and* V. A. ZAKHAROV

ABSTRACT. Bivalves of the genera *Praebuchia* and *Buchia* described here occur in great abundance in the Oxfordian to Valanginian Stages of East Greenland. Fifteen species have been identified. Their stratigraphic range is roughly the same as in other Arctic areas, and a detailed zonation based on buchiid bivalves seems to be valid from Arctic Canada over East Greenland to Andøy, Svalbard, Petshora River basin, Subarctic Urals, and northern Siberia. The following zones and beds have been recognized in East Greenland: The Upper Oxfordian *Praebuchia kirghisensis* Zone, the Kimmeridgian *Buchia concentrica* and *B. tenuistriata* Zones, the Middle Volgian *B. mosquensis* Zone and *B. russiensis* beds, the Upper Volgian *B. fischeriana* beds, the Upper Volgian–lowermost Ryazanian *B. unschensis*–*B. terebratuloides* beds, the Lower Ryazanian *B. okensis* Zone, the Upper Ryazanian *B. volgensis* Zone, the uppermost Ryazanian–lower Lower Valanginian *B. inflata* Zone, the upper Lower Valanginian *B. keyserlingi* Zone, the Upper Valanginian–(?) Hauterivian *B. sublaevis* and *B. crassicollis* Zones.

THE genus *Buchia* has been recognized at many localities in the Upper Jurassic and Lower Cretaceous of East Greenland (text-fig. 1). Madsen (1904), Ravn (1911), Spath (1936, 1947, 1952), Frebold (1933), Jeletzky (1965), Surlyk and Clemmensen (1975) and Surlyk (1973) all described and figured species of *Buchia*. Most of this material is restricted to scattered finds. A biostratigraphic scheme incorporating figured species of *Buchia* based on a large material collected in measured sections was constructed by Surlyk (1978*a*, *b*), and the present paper is the first monographic account of the Greenland material of this stratigraphically important genus, and its predecessor *Praebuchia*. The material was collected by one of us (F.S.) in south Jameson Land in 1970 and 1971 and in Kuhn Ø and Wollaston Forland in 1974 (text-fig. 1 and fig. 9 in Surlyk 1978*a*). Material collected by F. Fürsich on Milne Land in 1977 has also been incorporated.

Species of *Praebuchia* and *Buchia* occur scattered throughout the Upper Oxfordian–Kimmeridgian dark mudstones of the Hareelv and Bernbjerg Formations (text-figs. 1, 2; Table 1) (Surlyk *et al.* 1973; Surlyk 1977). The shallow marine, coarse sandstones of the Lower Volgian–Lower Valanginian Raukelv Formation and the slightly deeper water silt- and sandstones of the Ryazanian–Lower Valanginian Hesteelv Formation (Surlyk 1973) contain a more diverse *Buchia* fauna. The greatest density and diversity are, however, reached in the relatively deep-water conglomerates, sandstones, and mudstones of the Middle Volgian–Valanginian Wollaston Forland Group (Surlyk 1978*a*).

Some uncertainty still exists concerning the stratigraphic nomenclature across the Jurassic–Cretaceous boundary. The deposits of the Boreal faunal realm cannot yet be precisely dated within the framework of the Tithonian–Berriasian Stages of the Tethyan realm. Russian authors generally use the Volgian as the final Jurassic stage and the Berriasian as the basal Cretaceous stage in the boreal USSR. Casey (1973) suggested that the Volgian and Berriasian Stages overlapped and advocated the use of the Ryazanian Stage for the basal Cretaceous deposits until Tethyan–Boreal correlations were satisfactorily established. This usage has been followed in all subsequent work on the Jurassic–Cretaceous boundary strata in East Greenland (Surlyk *et al.* 1973; Surlyk 1973, 1977; 1978*a*, *b*; Birkelund, Callomon and Fürsich 1978).

[Palaeontology, Vol. 25, Part 4, 1982, pp. 727–753, pls. 72–77.]

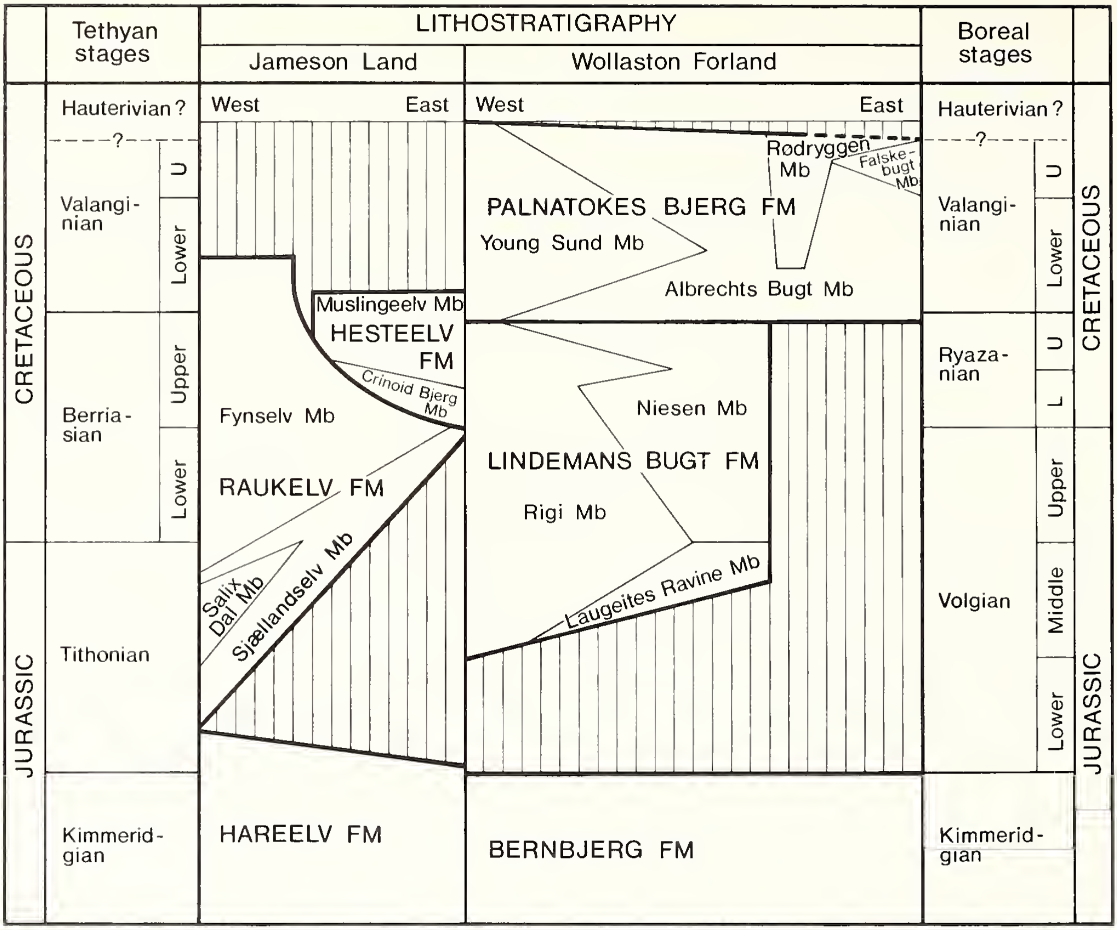
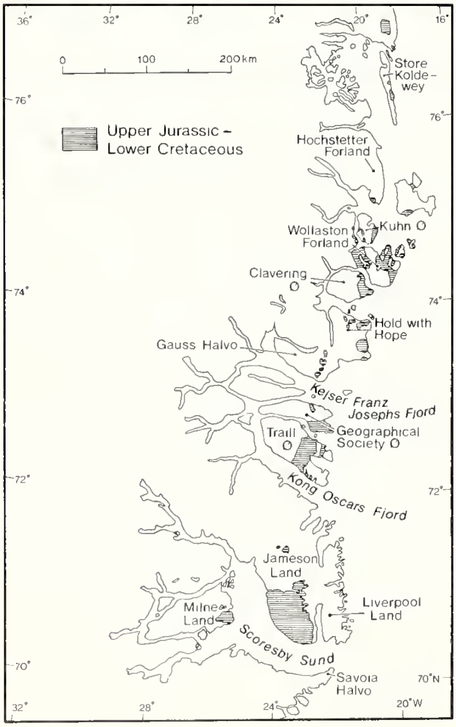
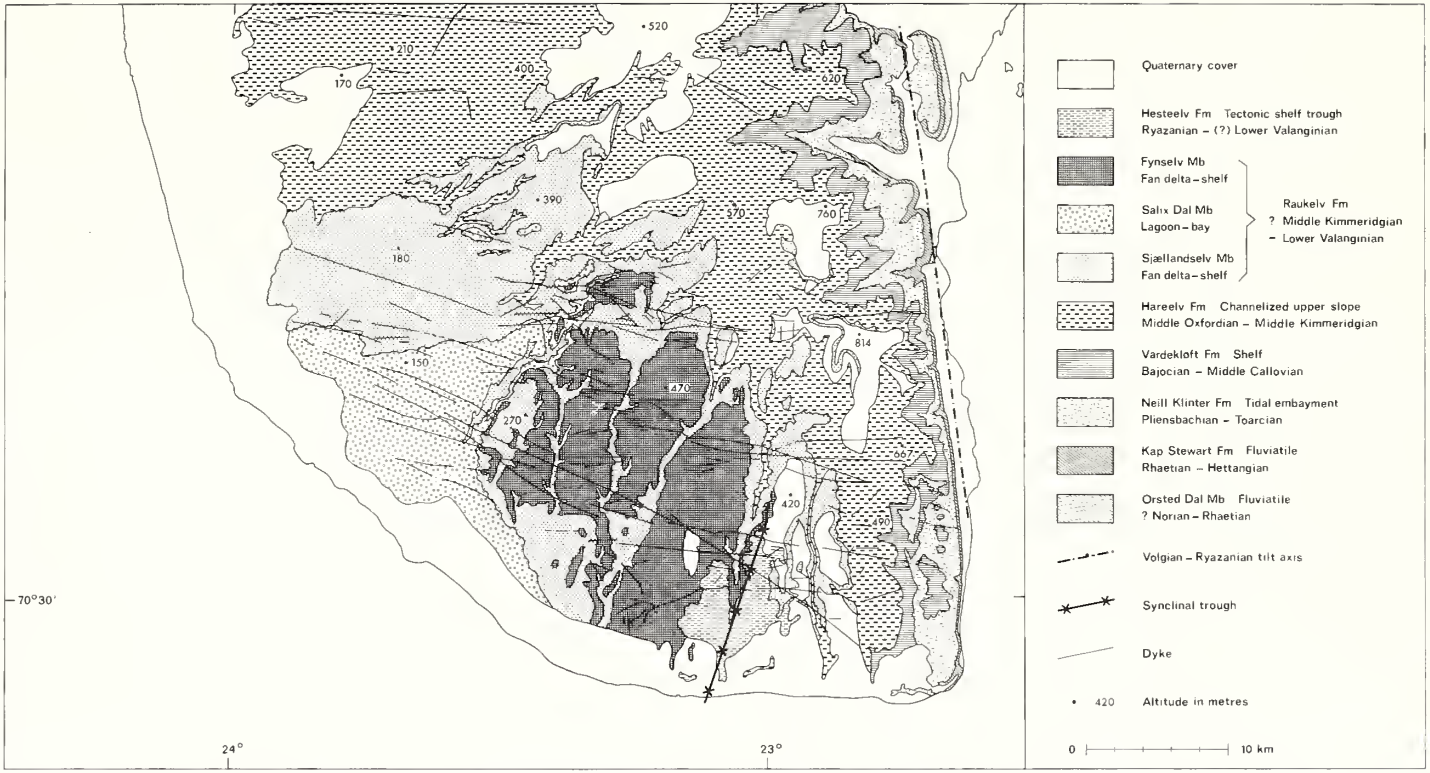


TABLE 1. Lithostratigraphy of the Jurassic–Cretaceous boundary sequences in Jameson Land and Wollaston Forland, East Greenland.



TEXT-FIG. 1. Map showing the localities mentioned in the text and the distribution of the Upper Jurassic–Lower Cretaceous *Buchia*-bearing sediments.



TEXT-FIG. 2. Simplified geologic map of southern Jameson Land showing distribution of the Jurassic–Cretaceous boundary strata and main synsedimentary structural features. Modified from unpublished GGU map compiled by F. Surlyk and T. Birkelund.

It is therefore also used in the present paper, although Zakharov (1981) in his monograph on *Buchia* of the Arctic USSR follows the general Russian practice. It should, however, be noted that Berriasian *sensu Rossico* is identical with the Ryazanian as defined on the Russian Platform (Casey 1973) and more or less identical with Berriasian/Ryazanian as used in Siberia (see Table 1).

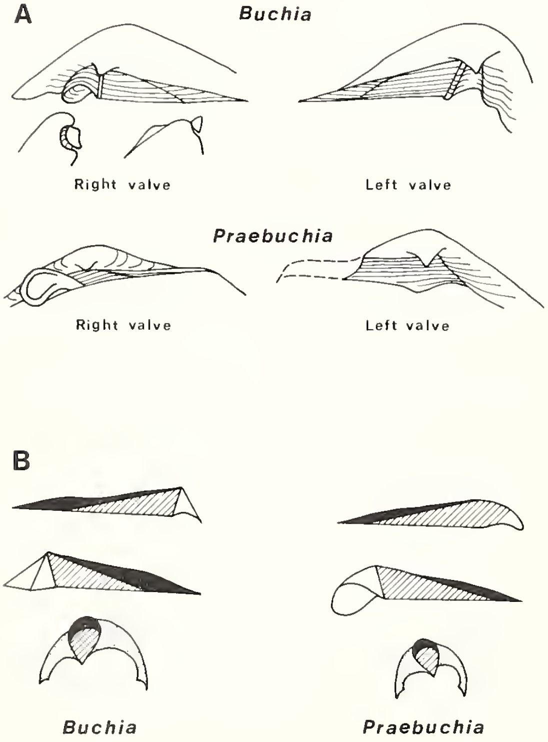
The lithostratigraphic nomenclature follows Surlyk *et al.* (1973) and Surlyk (1973, 1977, 1978*a*) and the majority of the sections where buchiid bivalves have been collected are figured in these papers.

SYSTEMATIC PALAEONTOLOGY

Boreal buchiid bivalves include two genera: *Praebuchia* Zakharov (1981) (Callovian–Oxfordian) and *Buchia* Rouillier (1845) (Oxfordian–Hauterivian) (text-fig. 3). In *Praebuchia* five species are recognized, while *Buchia* is represented by more than thirty species. The main difference between the two genera lies in the morphology of the hinge.

In *Praebuchia* the ligamental area is placed in the commissure plane, while in *Buchia* it forms an angle with this plane. *Praebuchia* is furthermore characterized by continuous grooves on the ligamental area anteriorly to the umbo, while in *Buchia* they are interrupted by a transverse ridge from the umbo (text-fig. 3). The ligament of *Praebuchia* was internal, whereas it was partly external in *Buchia*. *Buchia* possesses a well-developed byssal notch, while the margin of the ligamental area of *Praebuchia* is only slightly curved to allow the passage of an anterior auricle (Zakharov 1981).

Buchiid bivalves are characterized by a rapid rate of evolutionary change, and show a wide geographical distribution within the Late Jurassic–Early Cretaceous of the Boreal Realm, where they occur in a wide variety of facies. Taken together, these features make buchiid bivalves extremely



TEXT-FIG. 3. A, hinge structure in *Buchia* (from Zakharov 1981, fig. 5) and *Praebuchia* (from Zakharov 1981, fig. 26). B, comparison of ligament structure and position in *Buchia* and *Praebuchia*. Upper row, left valves; middle row, right valves; lower row, transverse sections. Lamellar layer is shown in black, and fibrous layer is cross-hatched. The main portion of the shells is indicated with stippled ornamentation.

valuable for stratigraphic purposes and they have accordingly received considerable attention for more than a hundred years.

This has led to a proliferation of names, and at present about 150 specific names have been founded within the genus *Buchia* alone. This extreme splitting is, however, opposed by another group of workers, who have used a very broad species concept. Either approach by itself may be detrimental for sound stratigraphic work, and the taxonomy at species level has to be based on studies of large, well-preserved populations. A discussion of these problems is given by Zakharov (1981). Full synonymy lists are also given for each species by Zakharov (1981) and here we only include earlier references from Greenland.

Family BUCHIIDAE Cox, 1953

Genus PRAEBUCHIA Zakharov, 1981

Type species. Praebuchia orientalis Zakharov, 1981

Range. Upper Callovian–Lower Oxfordian, northern Siberia.

Praebuchia kirghisensis (Sokolow, 1902)

Plate 72, figs. 1–3

1911 *Aucella kirghisensis* Ravn, p. 455, pl. 32, fig. 2.

Material. About ten poorly preserved specimens from Wollaston Forland, sections 38 and 41 in Surlyk (1977), and more than forty well-preserved specimens from Milne Land collected by F. Fürsich in 1977. Includes GGU 139450 (cf.), GGU 139451 (cf.) = MGUH 15341, GGU 139480 (cf.), GGU 235458 = MGUH 15348 (F. Fürsich coll.), GGU 235459 = MGUH 15349 (F. Fürsich coll.).

Remarks. Both casts and preserved valves of this equivalved species are easy to determine because of the lack of concentric ribs, their almost smooth surfaces, and moderately oblique angle (60°) between the hinge and median line. The shell is considerably inflated (Pl. 72, figs. 1, 2). The specimens from Milne Land are almost identical with specimens from Petshora River and Moscow region figured by Zakharov (1981, pl. 2).

Stratigraphical occurrence. The Milne Land material is from the Aldinger Elv Member (Upper Oxfordian Zones of *Amoeboceras glosense* and *A. serratum*). The Wollaston Forland specimens occur in the Upper Oxfordian part of the Bernbjerg Formation (*A. serratum* and *A. regulare* Zones). Ravn's (1911) specimen from Store Koldewey is from the Upper Oxfordian Kloft I Formation (Tables 2, 3).

In the northern part of the northern Eurasian Urals the species occurs throughout the Oxfordian but reaches peak abundances in the Upper Oxfordian (*A. alternans Zone*).

Genus BUCHIA Rouillier, 1845

Type species. Avicula mosquensis von Buch, 1844, p. 537.

Range. Lower–Middle Volgian of the Russian Plain.

Buchia concentrica (J. de C. Sowerby, 1829)

Plate 72, fig. 5

1911 *Aucella bronni* Ravn, p. 455, pl. 32, fig. 5.
1911 *Aucella sinzovi* Ravn, p. 456, pl. 32, fig. 3.
1911 *Aucella* cf. *reticulata* Ravn, p. 458, pl. 32, fig. 4.
1935 *Aucella* aff. *bronni* Spath, p. 53, pl. 3, fig. 2; pl. 8, fig. 3.

Material. About ten specimens from Kuhn Ø and Wollaston Forland (sections 1, 8, 40 in Surlyk 1977). Includes GGU 139305, GGU 139331, GGU 139332 = MGUH 15329, GGU 139471 (cf.).

Remarks. The species is characterized by its distinct radial ribs crossed by concentric ribs resulting in the formation of reticulate ornamentation. The upper part of the right valve is slightly concave in typical specimens. The shell is strongly oblique (Pl. 72, fig. 5). Poorly preserved specimens can be mistaken for *B. tenuistriata.*

Stratigraphical occurrence. Upper Oxfordian of Milne Land and Store Koldewey, and Kimmeridgian of Milne Land, Wollaston Forland, and Kuhn Ø (up to and including the Zone of *Aulacostephanus mutabilis*) (Tables 2, 3).

B. concentrica has the widest geographic distribution within the Boreal Realm of the Oxfordian–Lower Kimmeridgian species of *Buchia.* It is particularly abundant in the Lower Kimmeridgian (Zones of *Pictonia baylei* and *Rasenia cymodoce*). The specimens from the Upper Kimmeridgian of East Greenland (*A. mutabilis* Zone) are poorly preserved and the determination is questionable.

Buchia lindstroemi (Sokolow, 1908)

Plate 72, fig. 4

Material. Well-preserved internal mould of one right and one left valve from Milne Land collected by T. Birkelund and J. H. Callomon. Includes GGU 234071 = MGUH 15347 (F. Fürsich coll.)

Remarks. The species is characterized by its large adult size, strongly oblique shape, and ornamentation comprising strong closely but irregularly spaced folds with superimposed ribs. The less prominent radial ornamentation consists of weak striae.

Stratigraphical occurrence. In East Greenland the species has only been found in the Lower Kimmeridgian. This rare species occurs in the Upper Oxfordian–Lower Kimmeridgian of Eurasia and northern Alaska (Imlay 1959). It is everywhere associated with *B. concentrica,* but in northern Siberia ammonite evidence confirmed occurrences only in the Lower Kimmeridgian.

Buchia tenuistriata (Lahusen, 1888)

Plate 72, figs. 6–11; Plate 73, figs. 1, 2

1911 *Aucella tenuistriata* Ravn, p. 458, pl. 32, fig. 7.

Material. About twenty specimens from Kuhn Ø (section 8, Surlyk 1977), and more than fifty specimens from the collection of Maync (1947). The latter are from a locality on the west coast of Kuhn Ø, but the exact location

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EXPLANATION OF PLATE 72

All specimens except 9 are figured in natural size.

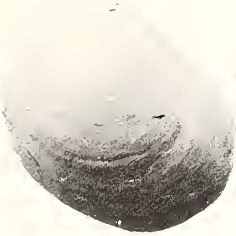
Figs. 1–2. *Praebuchia kirghisensis* (Sokolow). 1, GGU 235458 (F. Fürsich coll. 1977). A, lateral view of left valve, internal mould. B, dorsal view. C, right valve. 2, GGU 235459 (F. Fürsich coll. 1977). A, left valve. B, dorsal view. C, right valve.

Fig. 3. *Praebuchia* cf. *kirghisensis* (Sokolow). GGU 139451. Internal cast of a large, strongly deformed right valve. Bernbjerg Formation, *Amoeboceras* (*P.*) *serratum* Zone. Section 38, 228 m in Surlyk 1977, fig. 16. Cardiocerasdal, south-west Wollaston Forland.

Fig. 4. *Buchia lindstroemi* (Sokolow). GGU 234071 (Fürsich coll. 1977). A, lateral view of left valve. B, lateral view of right valve, probably the same individual as in A.

Fig. 5. *Buchia concentrica* (J. de C. Sowerby). GGU 139332. Internal cast of right valve with flattened lower part. Bernbjerg Formation, *Aulacostephanus mutabilis* Zone. Section 8, 168 m in Surlyk 1977, fig. 24. Eastern slope of Bernbjerg, south-west Kuhn Ø.

Figs. 6–11. *Buchia tenuistriata* (Lahusen). 6, Internal cast of right valve, and 7, of compressed left valve, GGU 139472. Bernbjerg Formation, *Rasenia cymodoce–Aulacostephanus mutabilis* Zones. Section 40, 172 m in Surlyk 1977, fig. 31. Cardiocerasdal, south-west Wollaston Forland. 8, 10, GGU 139336. Internal moulds of two left valves (8), and a right valve (10). Bernbjerg Formation. *A. mutabilis–A. eudoxus* Zones. Section 8, 273 m in Surlyk 1977, fig. 24. Eastern slope of Bernbjerg, south-west Kuhn Ø. 9, 11 (Nos. 1240, 87, Maync coll.). Internal moulds of three right valves. Bernbjerg Formation, western Kuhn Ø. Exact locality unknown.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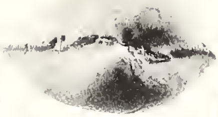
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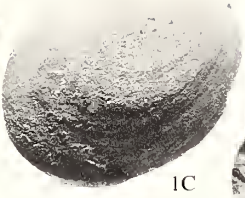
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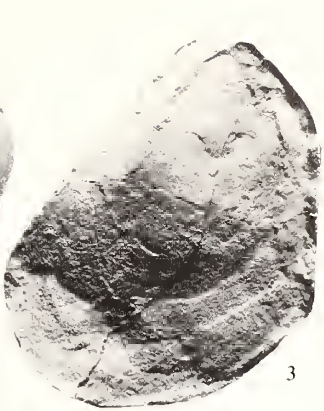
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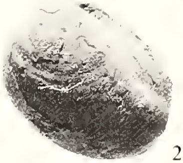
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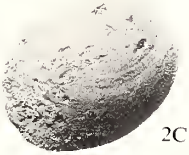
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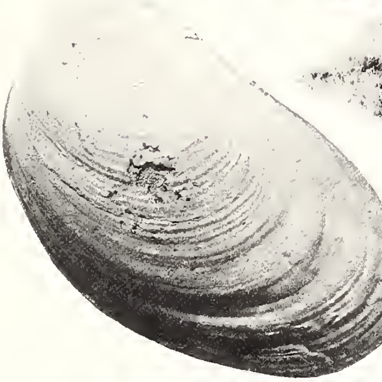
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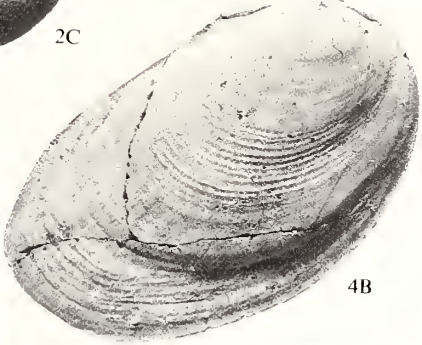
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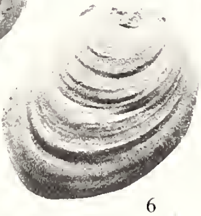
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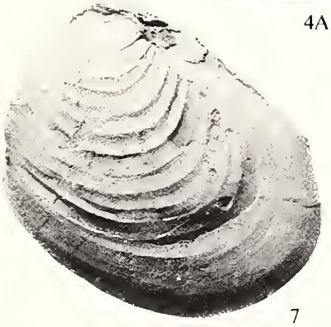
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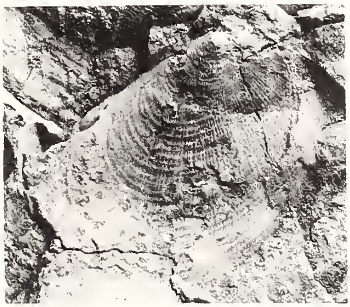
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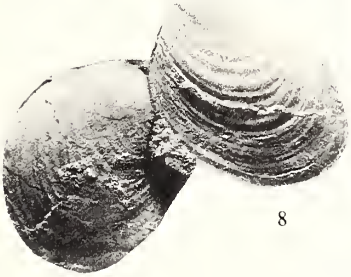
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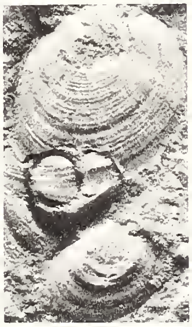
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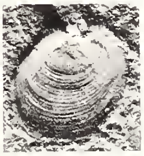
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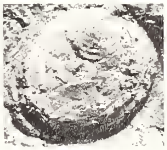
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SURLYK and ZAKHAROV, *Buchia*, *Praebuchia* is unknown. Includes GGU 139330 = MGUH 15328, GGU 139331 (cf.), GGU 139332 (cf.), GGU 139336 = MGUH 15330, GGU 139337 (cf.), GGU 139458 (cf.), GGU 139472 = MGUH 15342, (1240–87, Maync coll.).

Remarks. B. tenuistriata is closely related to *B. mosquensis* (Pavlow 1907, p. 22, pl. 2, figs. 5–8) and is quite often mistaken for this species. Both species are extremely variable and satisfactory identifications can be made only on large samples. *B. tenuistriata* is characterized by its narrower and less oblique shell and in possessing more well-developed radial striation. The radial keel of the right valve is only feebly developed or totally absent. The left umbo is slightly prosogyrate and is obliquely truncated anteriorly.

Stratigraphical occurrence. The species occurs in the Lower and in particular Upper Kimmeridgian of Kuhn Ø, and in the Kimmeridgian at Danmarks Havn in southern Germania Land (Sykes and Surlyk 1976). It occurs in great abundances in the Upper Kimmeridgian in the northern part of the European USSR and in northern Asia, but in some localities such at Petshora River it also occurs in the Lower Kimmeridgian together with *B. concentrica*.

Buchia mosquensis (von Buch, 1844)

Plate 73, figs. 3, 4

1904 *Aucella pallasii* Madsen, p. 178, pl. 6, fig. 7.
1936 *Buchia mosquensis* Spath, p. 98, pl. 42, fig. 1 (not 1*e*).

Material. About ten specimens from southern Jameson Land. Very common in the Perna Ryggen Member of Milne Land (F. Fürsich coll.). Includes GGU 143120 = MGUH 15346.

Remarks. The specimens are typical representatives of the species. The right valve possesses a keel which divides the surface of the valve into flat posterior and anterior parts. The anterior margin of the shell is broadly rounded. The left valve is inflated and has a twisted beak.

Stratigraphical occurrence. On Jameson Land the species occurs in the mainly Middle Volgian Sjællandselv Member of the Fynselv Formation (Table 1) (Surlyk *et al.* 1973) and in sandstones presumably of the same age at Aucellaelv (Madsen 1904). The material from Milne Land described by Spath (1936) is also from the Middle Volgian, and collections by F. Fürsich can be dated as belonging to the *Dorsoplanites ilovaiskii*, *D. maximus*, and *Crendonites* sp. Zones (Table 2).

In northern Eurasia the species has its first appearance in the Upper Kimmeridgian but reaches its main abundance in the Lower and Middle Volgian. It has never been found in the Upper Volgian. The species has been reported from the Lower and Upper Kimmeridgian by Paraketsov (1968), but his material can in our opinion be referred to *B. tenuistriata*.

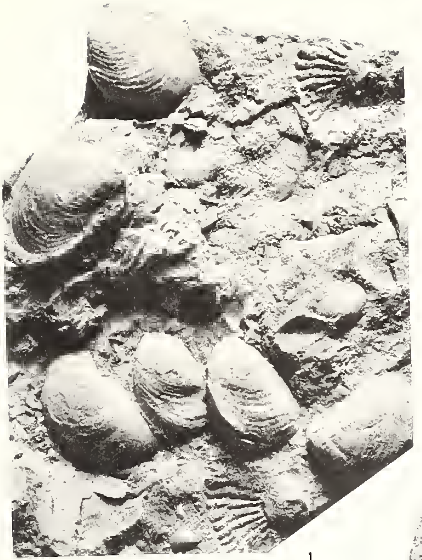
EXPLANATION OF PLATE 73

All specimens are figured in natural size.

Figs. 1–2. *Buchia tenuistriata* (Lahusen). GGU 139330. 1, internal moulds of six left valves and, 2, of a right valve. Bernbjerg Formation, *Rasenia cymodoce* Zone. Section 8, 85 m in Surlyk 1977, fig. 24. Eastern slope of Bernbjerg, south-west Kuhn Ø.

Figs. 3–4. *Buchia mosquensis* (von Buch). GGU 143120. All specimens are internal moulds. 3*a*, lateral view of left valve. 3*b*, dorsal view of umbonal part of same valve as in 3*a*. 4, lateral view of right valve. Raukelv Formation, Sjællandselv Member, Middle Volgian, 305 m above sea level. Southern Jameson Land.

Figs. 5–12. *Buchia russiensis* (Pavlow). GGU 139393. All specimens are internal moulds. 5–8, lateral view of right valves. 9–12, lateral view of left valves. Lindemans Bugt Formation, Laugeites Ravine Member, *Epilaugeites vogulicus* Zone. Section 20, 88 m in Surlyk 1978*a*, appendix. Niesen, northern Wollaston Forland.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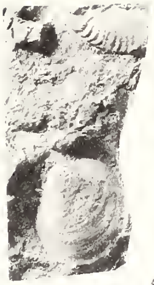
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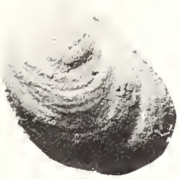
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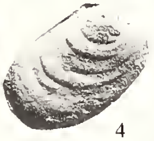
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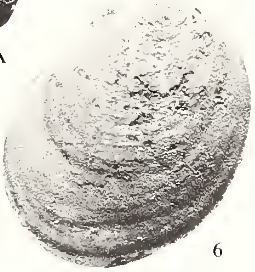
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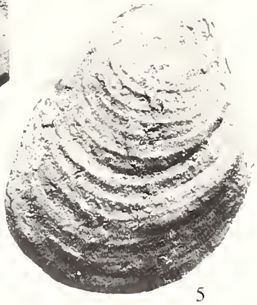
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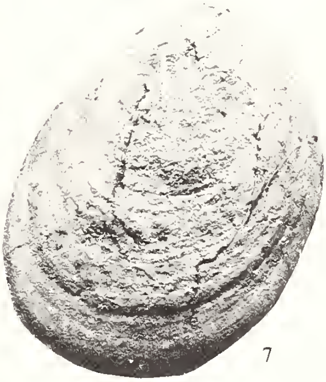
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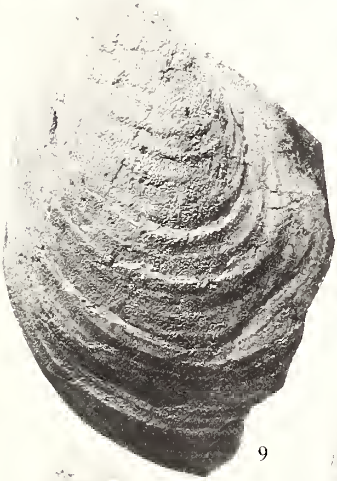
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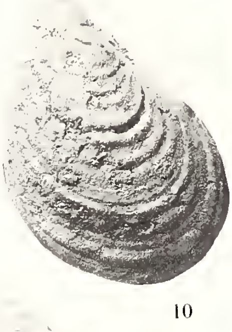
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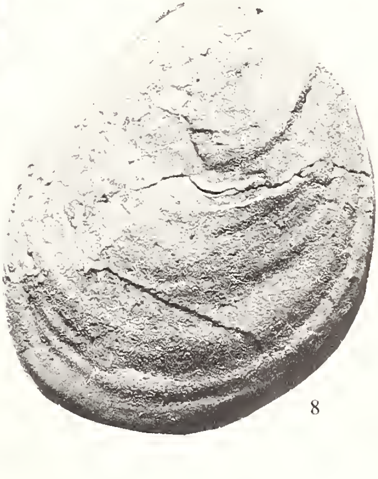
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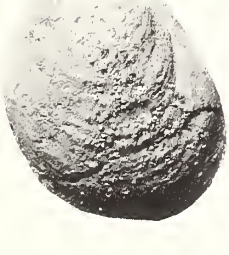
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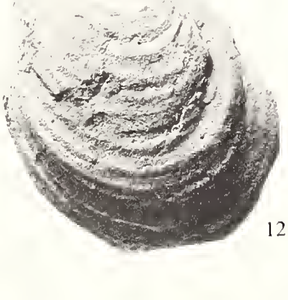

12

SURLYK and ZAKHAROV, *Buchia*

Buchia russiensis (Pavlow, 1907)

Plate 73, figs. 5–12; Plate 74, figs. 1–4

1978*a* *Buchia* ex gr. *volgensis* Surlyk, p. 30, pl. 1, fig. 2; pl. 2, fig. 3.

Material. About sixty casts and moulds of left and right valves from western Kuhn Ø, section 5 in Surlyk (1978*a*) and locs. 7, 9, 10, 11 of Donovan (1964), and several casts and moulds from northern Wollaston Forland, section 20 of Surlyk (1978*a*). Includes GGU 139317 = MGUH 15327, GGU 139318, GGU 139319 (cf.), GGU 139321 (cf.), GGU 139323 (cf.), GGU 139393 = MGUH 15333, GGU 139432 = MGUH 15338, GGU 139433 (cf.).

Remarks. *B. russiensis* is geographically widespread and shows great variation both within and between populations. The present material is most closely related to populations from the Petshora and Volonga Rivers (*D. maximus–Laugeites groenlandicus* Zones) (Zakharov 1981, pl. 15). The main characteristic of this type is the large size, and the left valves show great resemblances to *B. volgensis* in being inflated and in possessing a large incurved beak. Some of the left valves and most of the right valves correspond to the form called *B. russiensis* var. *nniovnikensis* by Jeletzky (1965, pl. 1, figs. 4, 5, 9). Several right valves are close to *B. fischeriana* from northern Siberia (Zakharov 1981, pl. 21, fig. 22) and from Arctic Canada (Jeletzky 1966, pl. 8, figs. 2–6, 9), but differ in not having regular concentric ribs.

Stratigraphical occurrence. All the material comes from the Middle Volgian Zones of *L. groenlandicus* and *Epilaugeites vogulicus*. Outside East Greenland *B. russiensis* occurs in the Middle Volgian and the lowermost Upper Volgian (Zone of *Kachpurites fulgens*) of the Petshora River basin. Populations composed of large-sized specimens are characteristic of the uppermost Middle Volgian.

Buchia fischeriana (d'Orbigny, 1845)

Plate 74, figs. 5, 6

1978*a* *Buchia* aff. *fischeriana* Surlyk, pl. 4, fig. 12 (some of the specimens on the slab of sandstone may belong to *B. unschensis*).

EXPLANATION OF PLATE 74

All specimens are figured in natural size.

Figs. 1–4. *Buchia russiensis* (Pavlow). 1–3, GGU 139317. All specimens are internal moulds. 1–2, lateral view of left valves. 3, lateral view of right valve. Lindemans Bugt Formation, Laugeites Ravine Member, *Laugeites groenlandicus* Zone. Section 5, 10 m in Surlyk 1978*a*, appendix. Laugeites Ravine, western Kuhn Ø. 4, GGU 139432. A, lateral view of left valve and B, dorsal view of umbonal part. Lindemans Bugt Formation, Laugeites Ravine Member, probably *Laugeites groenlandicus* Zone. West of Sillerendal, northern Wollaston Forland.

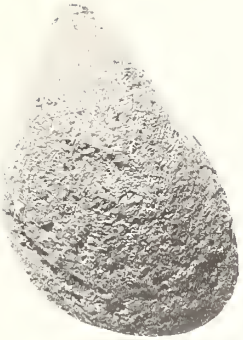
Figs. 5–6. *Buchia fischeriana* (d'Orbigny). GGU 139417. 5, lateral view of left valve and 6, of right valve. Lindemans Bugt Formation, Niesen Member, '*Virgatosphinctes*' *tenuicostatus* beds. Section 20, 175–180 m in Surlyk 1978*a*, appendix.

Figs. 7–9. *Buchia terebratuloides* (Lahusen). GGU 139429. 7*a*, *b*, *c*, lateral, posterior, and dorsal view of left valve. 8, lateral view of left valve. 9, lateral of right valve. Lindemans Bugt Formation, Rigi Member, Upper Volgian, Section 14, 120 m in Surlyk 1978*a*, appendix.

Fig. 10. *Buchia terebratuloides* (Lahusen). GGU 138177. Lateral view of right valve. Hesteelv Formation, Muslingeelv Member, *Hectoroceras kochi* Zone. Muslingeelv, southern Jameson Land.

Figs. 11–12. *Buchia unscheusis* (Pavlow). GGU 138182. 11, lateral view of right valve. 12A, lateral and B, anterior view of left valve. Hesteelv Formation, Muslingeelv Member, *Hectoroceras kochi* Zone. Muslingeelv, southern Jameson Land.

Figs. 13–14. *Buchia unschensis* (Pavlow). GGU 139437. Lateral view of right valves. Lindemans Bugt Formation, Upper Volgian, '*Virgatosphinctes*' *tenuicostatus* beds. West of Sillerendal, 235 m above sea level, northern Wollaston Forland.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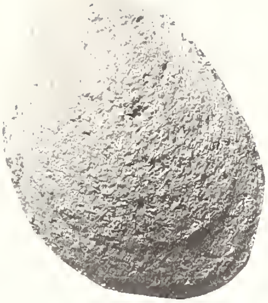
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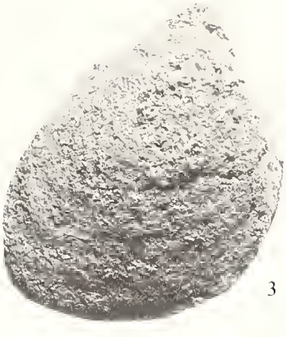
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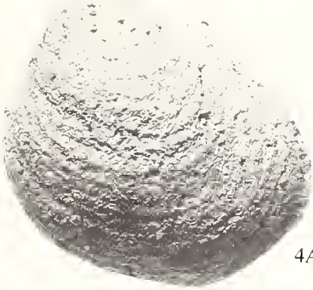
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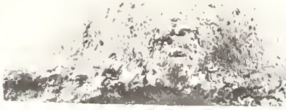
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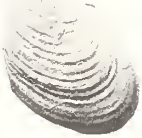
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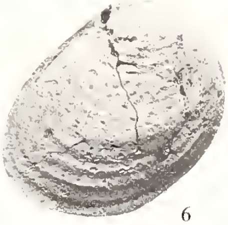
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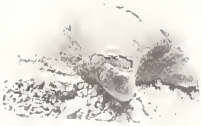
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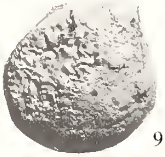
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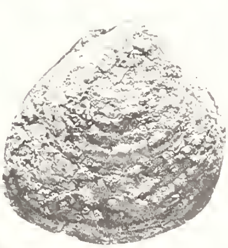
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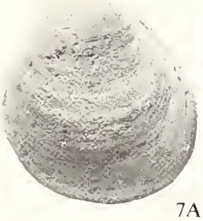
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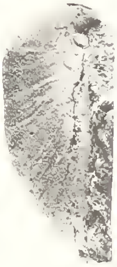
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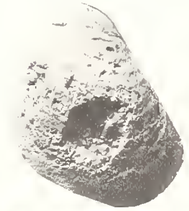
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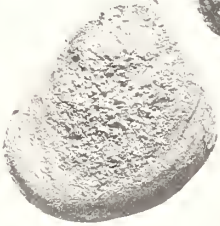
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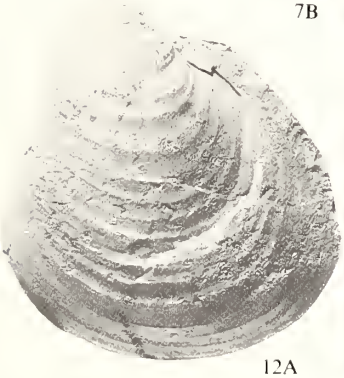
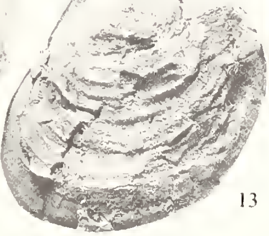

12A

12B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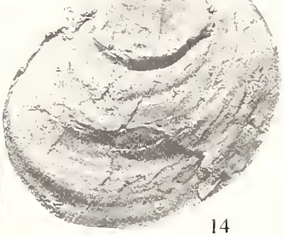

14

SURLYK and ZAKHAROV, *Buchia*

Material. About thirty specimens from Wollaston Forland, section 20 of Surlyk (1978*a*), including GGU 139417 = MGUH 15334, GGU 139428.

Remarks. Correct identification is difficult because the material comprises only moulds of flattened densely packed specimens. The typical regular concentric ribs are, however, well preserved on a number of specimens, and the characteristic slight increase in obliquity of both valves can also be observed.

Stratigraphical occurrence. In East Greenland the species occurs in the top Middle Volgian (*E. vogulicus* Zone) and Upper Volgian ('Virgatosphinctes' tenuicostatus beds).

B. fischeriana has often been observed in the uppermost Middle Volgian (*Epivirgatites nikitini* Zone), in the Upper Volgian, and in the basal Ryazanian of the central part of the Russian Plain. In northern Siberia the species has its greatest abundance in the Upper Volgian, where it occurs together with *B. unschensis*, *B. terebratuloides*, and *B. obliqua*. It is very rare in the basal Ryazanian of northern Siberia, but occurs in the Middle Volgian–Lower Ryazanian of Peary Land, North Greenland.

Buchia terebratuloides (Lahusen, 1888)

Plate 74, figs. 7–10

1947 *Buchia* cf. *terebratuloides* Spath, pl. 2, figs. 7, 8.
1947 *Buchia volgensis* Spath, pl. 1, fig. 9; pl. 3, fig. 5*c* (only).
1952 *Buchia volgensis* Spath, pl. 3, figs. 6, 7; pl. 4, fig. 4.

Material. More than fifty specimens from Wollaston Forland (sections 14, 20, and 45 of Surlyk 1978*a*) and southernmost Jameson Land. In addition, the samples contain many poorly preserved specimens which cannot be safely determined but belong either to *B. terebratuloides* or to *B. unschensis*. Includes GGU 138177 = MGUH 15324, GGU 138181, GGU 138182, GGU 138183, GGU 138184 (cf.), GGU 138185, GGU 138187, GGU 138191, GGU 138193, GGU 139402, GGU 139403, GGU 139429 = MGUH 15337, GGU 139491, GGU 139502 (cf.).

Remarks. The specimens are mainly of medium size, slightly oblique, and relatively high. Both valves show equal convexity, but the beak of the left valve is more massive than of the right valve and is furthermore elongated and overhangs the hinge line. The concentric ribs are irregularly spaced and not uniform in relief. They are more weakly developed on the cast than on the outer surface of the shell.

Stratigraphical occurrence. B. terebratuloides occurs in the upper part of the Volgian ('*V.*' *tenuicostatus* beds) and in the Lower Ryazanian (*P. maynci* and *Hectoroceras kochi* Zones). On the Russian Platform this species appears in the lowermost Upper Volgian (*K. fulgens* Zone), reaches its greatest abundance in the Upper Volgian *Craspedites* beds, and occurs only rarely in the lowermost Ryazanian. In northern Siberia and in the Petshora River basin *B. terebratuloides* mainly characterizes the Upper Volgian. The same stratigraphic distribution is found at the Pacific coast of North America and in Arctic Canada (Jones, Bailey and Imlay 1969; Jeletzky 1973).

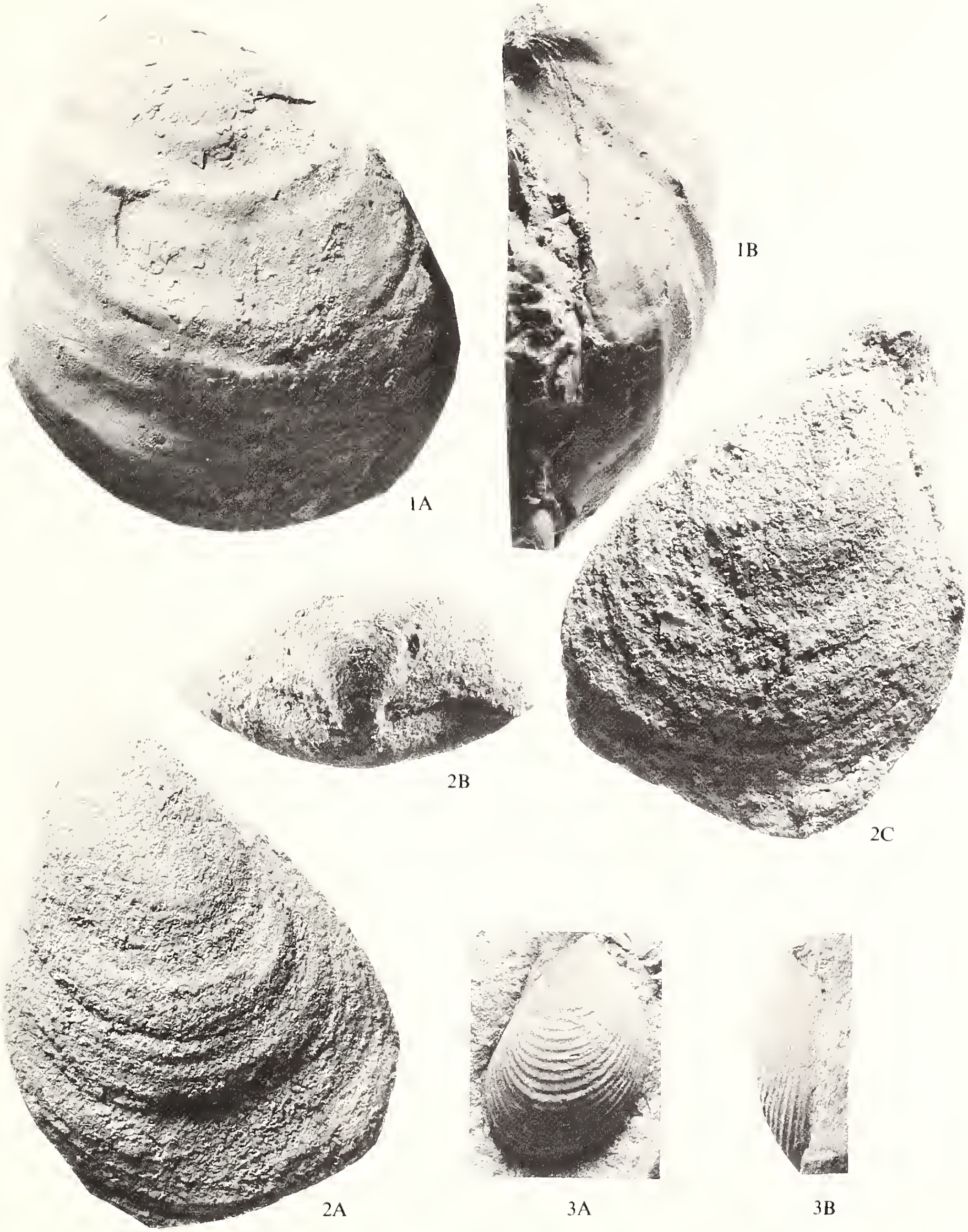
EXPLANATION OF PLATE 75

All specimens are internal moulds and are figured in natural size.

Fig. 1. *Buchia okensis* (Pavlow). GGU 138190. A, lateral view and B, anterior view, of left valve. The specimen was figured by Surlyk 1973, pl. 1, fig. 1. Hesteelv Formation, Muslingeelv Member, *Hectoroceras kochi* Zone, Muslingeelv, southern Jameson Land.

Fig. 2. *Buchia volgensis* (Lahusen). GGU 143101. A, lateral view and B, dorsal view of left valve. C, lateral view of right valve. Raukelv Formation, Fynselv Member, top beds, Upper Ryazanian, 420 m above sea level. West of Fynselv, upper reach, southern Jameson Land.

Fig. 3. *Buchia inflata* (Lahusen). GGU 139439. A, lateral and B, anterior view of right valve. Palnatokes Bjerg Formation, Albrechts Bugt Member, Lower Valanginian, Section 35, 430 m, south side of Niesen, Wollaston Forland.



SURLYK and ZAKHAROV, *Buchia*

Buchia unschensis (Pavlow, 1907)

Plate 74, figs. 11–14

1947 *Buchia volgensis* Spath, p. 34, pl. 3, fig. 5*a*, *b*; (?) pl. 4, figs. 8–9; pl. 5, figs. 1–2.
1952 *Buchia volgensis* Spath, pl. 1, fig. 1; pl. 4, figs. 5, 7.

Material. More than twenty specimens (see also under *B. terebratuloides*) from Wollaston Forland (section 20 of Surlyk, 1978*a*) and southern Jameson Land. Includes GGU 138177 (cf.), GGU 138181, GGU 138182 = MGUH 15325, GGU 138185 (cf.), GGU 138187, GGU 138189 (cf.), GGU 139402, GGU 139403, GGU 139437 = MGUH 15339, GGU 139502 (cf.), GGU 143065 (cf.).

Remarks. The specimens are of medium to moderately large size for the species. The shell has a rounded non-oblique shape. The surface is covered by regularly spaced ribs of equal strength. The posterior part is broad and wing-like. The better-preserved specimens are strongly reminiscent of specimens from the lowermost *H. kochi* Zone of northern Siberia (Zakharov 1981, pl. 29, figs. 1–3). The only differences are the less convex valves, more narrow elongated beaks on the left valve, and less regular ribs of the East Greenland specimens. On the basis of these features Jeletzky (1973) referred the specimens figured by Spath (1947) to *B. terebratuloides* and *B.* sp. nov. aff. *okensis*.

Here we interpret the features as intraspecific variation within the Greenland material of *B. unschensis*.

Stratigraphical occurrence. In East Greenland the species occurs in the Upper Volgian ('*V.*' *tenuicostatus* beds) and Lower Ryazanian (*P. maynci–H. kochi* Zones). *B. unschensis* is widespread in the northerly (mainly Arctic) depositis of the Upper Volgian *Craspedites subditus* Zone and the Lower Ryazanian *H. kochi* Zone. It is even more abundant in the Jurassic–Cretaceous boundary beds in northern Siberia, Petshora River, Spitzbergen, North Greenland, and probably in Arctic Canada (Jeletzky 1966, Zakharov 1981). It occurs together with *Hectoroceras* sp. in the lower part of the Ryazanian at the Oka River (Mesezhnikov *et al.* 1977, 1979).

Buchia okensis (Pavlow, 1907)

Plate 75, fig. 1

1973 *Buchia okensis* Surlyk, pl. 1, fig. 1.

Material. Two specimens from southern Jameson Land, GGU 138190 = MGUH 15326, GGU 138191.

Remarks. Identification is somewhat difficult as the material comprises only incomplete left valves. The surface of the moulds is sculptured by a few coarse concentric folds, which are strongest at the anterior margin and become more smooth towards the posterior margin. The coarsely ribbed specimens closely resemble basal Ryazanian forms from the Pakhsa Peninsula, northern Siberia (Zakharov 1981, pl. 35, figs. 1, 2), Vancouver, British Columbia (Jeletzky 1965, pl. 6, figs. 1, 3–5), northern Alaska (Imlay 1961, pl. 7, figs. 12, 17–20) and Canadian Arctic Archipelago (Jeletzky 1964, pl. 1, fig. 1). The specimens from Jameson Land differ in having more irregularly spaced folds.

Stratigraphical occurrence. In East Greenland the species occurs in the Lower Ryazanian (*H. kochi* Zone). *B. okensis* is widespread in the boreal Berriasian (Ryazanian) of both northern Eurasia and northern America. According to most authors the appearance of *B. okensis* indicates the start of the Cretaceous. It is, however, not found in the *Chetaites sibiricus* Zone, nor in its time equivalent, the *Praetollia maynci* Zone (see Surlyk 1978*a*) in northern USSR (Petshora and Chatanga Rivers) and in East Greenland. It first appears at the base of the *H. kochi* Zone and the last rare specimens occur in the *Surites analogus* Zone (Zakharov 1981). No representatives of *B. okensis* have been found in the *Bojarkia mesezhnikovi* Zone.

Buchia volgensis (Lahusen, 1888)

Plate 75, fig. 2

1978*a* *Buchia volgensis* Surlyk, p. 32, pl. 6, figs. 1–5 (only).

Material. About seventy specimens from southern Jameson Land and Wollaston Forland, including GGU 139493, GGU 139503 (cf.), GGU 143028 (cf.), GGU 143094 (cf.), GGU 143101 = MGUH 15345, GGU 143143, GGU 137999 (cf.), GGU 138191 (cf.), GGU 139375, GGU 139376 (cf.), GGU 139400 (cf.), GGU 139407, GGU 139418 (cf.), GGU 139420 (cf.).

Remarks. The Greenland material is typical of this well-known species (see e.g. Zakharov 1981).

Stratigraphical occurrence. In East Greenland *B. volgensis* occurs throughout the Ryazanian except for the basal *Praetollia maynci* Zone. *B. volgensis* is extremely widespread in the Boreal and Subboreal Ryazanian. In northern USSR the species appears above the Jurassic–Cretaceous boundary at the base of the *H. kochi* Zone (Zakharov 1977, 1979), and most of the earlier identifications from the Upper Volgian in the Middle Siberia (Saks 1972) are erroneous. The alleged specimens of *B. volgensis* from the Upper Volgian can probably all be explained as misidentified specimens of *B. unschensis* (Zakharov 1981, pl. 3, fig. 4).

The species has the same stratigraphic range in northern North America (Jeletzky 1965). All the specimens from the *P. maynci* Zone of East Greenland described by Spath (1947, 1952) as *B. volgensis* belong to *B. unschensis* or *B. terebratuloides*, while some cannot be identified (Jeletzky 1973, p. 52). The specimens described as *B.* ex gr. *volgensis* from the upper part of the Middle Volgian and as *B. volgensis* from the Upper Volgian by Surlyk (1978*a*) are here referred to *B. russiensis* (Pavlow).

Buchia inflata (Lahusen, 1888)

Plate 75, fig. 3; Plate 76, fig. 1

1965 (?) *Buchia inflata* Jeletzky, pl. 1, figs. 7–8.
1978*a* *Buchia keyserlingi* Surlyk, p. 33, pl. 7, figs. 4–5, (?) 6.

Material. Twenty-two specimens from Wollaston Forland and Kuhn Ø, partly from sections 10, 15, and 53 in Surlyk (1978*a*). Including GGU 139348, GGU 139351, GGU 139356, GGU 139378 (cf.), GGU 139383 (cf.), GGU 139413, GGU 139439 = MGUH 15340, GGU 139352 = MGUH 15332.

Remarks. B. inflata is represented by medium- and moderately large-sized, subtriangular, high and almost equilateral specimens. The surface is covered by regularly spaced concentric ribs. Several of the specimens compare well with material from northern Siberia, Subarctic Urals, and Petshora River (Zakharov 1981, pls. 43–47) and from Andøy (Sokolow, 1912). The mode of growth of the right valve of several specimens (Surlyk 1978*a*, pl. 7, figs. 4, 5) much resembles *B. pacifica* from Vancouver, British Columbia (Jeletzky 1965, pl. 16, fig. 7), but strongly convex forms which are characteristic of samples from northern Siberia and British Columbia are absent from the Greenland material.

Stratigraphical occurrence. In East Greenland *B. inflata* occurs in the Lower Valanginian of Wollaston Forland and Kuhn Ø. The first appearance of *B. inflata* in northern Eurasia (Petshora and Cheta Rivers) is in the uppermost part of the *Bojarkia mesezhnikovi* Zone (uppermost Ryazanian). In northern Siberia the species reaches its greatest abundance in the Lower Valanginian (*Neotollia klimovskiensis Zone*) while it is very rare in uppermost Lower Valanginian.

Buchia keyserlingi (Trautschold, 1868)

Plate 76, figs. 2, 3; Plate 77, fig. 1

1874 *Aucella concentrica* var. *rugosa* Toula, p. 503, pl. 2, figs. 2–4.
1911 (?) *Aucella* sp. Ravn, p. 459, pl. 33, fig. 1.
1911 (?) *Aucella concentrica* Ravn, p. 461, pl. 32, figs. 9–10.
1911 (?) *Aucella piriformis* Ravn, p. 460, pl. 32, figs. 11, 12.
1965 *Buchia keyserlingi* Jeletzky, pl. 19, figs. 1, 2, 5, 7.
1975 (?) *Buchia keyserlingi* Surlyk and Clemmensen, pp. 67, 69, fig. 9.
1978*a* *Buchia keyserlingi* Surlyk, p. 33, pl. 8, fig. 4 (*non* pl. 7, figs. 4–6).
1978*b* *Buchia keyserlingi* Surlyk, p. 80, fig. 7E, F.

Material. More than 200 specimens from Kuhn Ø and Wollaston Forland (much of the material is from sections 10, 15, 18, 20, and 53 in Surlyk 1978*a*, and section 40 in Surlyk 1977). Including GGU 139349 (cf.), GGU 139350, GGU 139351 (cf.), GGU 139342 (cf.), GGU 139356, GGU 139357, GGU 139379 (cf.), GGU 139381, GGU 139382, GGU 139383 (cf.), GGU 139386 (cf.), GGU 139394, GGU 139395, GGU 139397 (cf.), GGU 139411, GGU 139412 (cf.), GGU 139413, GGU 139414, GGU 139421 (cf.), GGU 139440 (cf.), GGU 139441, GGU 139462 (cf.), GGU 139475, GGU 139476, GGU 139477, GGU 139478 (cf.), GGU 139499 (cf.), GGU 139504 (cf.), GGU 139511, GGU 139519, GGU 139522 (sp. juv.), GGU 139524, GGU 139525, GGU 139526, GGU 139528, GGU 139532 (cf.), GGU 139534 = MGUH 15344, GGU 139535 (cf.), GGU 143161 (cf.).

Remarks. B. keyserlingi is by far the most abundant species of *Buchia* from East Greenland and practically all the varieties described in the literature are represented.

The majority have a rounded outline and regularly spaced ribs (Pl. 76, fig. 2; Pl. 77, fig. 1; see also Surlyk and Clemmensen 1975, fig. 9; Surlyk 1978*b*, figs. 7E, F), near to the lectotype (Keyserling 1846, pl. 16, fig. 16; see also Zakharov 1981, pl. 50, fig. 4). These forms have in the earlier literature been called *B. keyserlingi* var. *sibirica* (Sokolow). Another form represented is close to the original specimen of Lahusen (1888, pl. 4, figs. 18–23; see also Zakharov 1981, pl. 54, fig. 3). Its main characteristic is the closely spaced ribs. The form is well known from Middle (?) Valanginian of the Arctic Canadian Archipelago (Jeletzky 1964, pl. 5, fig. 2) and from the *Temnoptychites syzranicus* Zone of the Petshora River basin (Zakharov 1981, pl. 55, fig. 4). *B. keyserlingi* var. *gigas* (Crickmay) is probably a gerontic form of this closely ribbed variety. Such large specimens have also been found in East Greenland (Jeletzky 1965, pl. 9, fig. 1; Surlyk 1978*a*, pl. 8, fig. 4) and have also been recorded from northern Siberia (Zakharov 1981, pl. 54, fig. 2) and Kong Karls Land (so-called variety *brasiliensis*, Blüthgen, 1936). A fairly rare variety with a smooth internal mould (Pl. 77, fig. 1) usually occurs together with ribbed varieties in the Lower Valanginian of the Anabar River, northern Siberia (Zakharov 1981, pl. 53). In large samples from eastern Wollaston Forland all transitions occur between the above-mentioned varieties.

B. piriformis and *B.* sp. of Ravn (1911) are represented by internal moulds of the left valves only and determination is thus not definitive. It should be noted, however, that these specimens have a high shell, smooth surface of the moulds, and that the middle part of the valves display a strong convexity. These features are highly reminiscent of *B. sublaevis* from the Upper Valanginian of the Petshora River basin (Zakharov 1981, pl. 58).

Stratigraphical occurrence. In East Greenland *B. keyserlingi* occurs in the Lower Valanginian of Kuhn Ø, Wollaston Forland, Hochstetter Forland, and probably Store Koldewey. *B. keyserlingi* is typical of the Boreal Lower Valanginian, where it occurs in great abundance. The species does not occur in the Ryazanian, but in large samples of Ryazanian *B. unschensis* or *B. volgensis* there will normally occur several specimens which strongly resemble *B. keyserlingi. B. keyserlingi* reaches its maximum abundance in the middle part of the Valanginian (*T. syzranicus* and *Polyptychites keyserlingi* Zones). The species is rare in the Upper Valanginian, where other species such as *B. sublaevis* have taken over. The youngest occurrence is in northern Germany (Westphalia and Lower Rhine), where rare *B.* ex gr. *keyserlingi* occur together with *Endemoceras* of Early Hauterivian Age (Kemper 1975).

Buchia sublaevis (Keyserling, 1846)

Plate 77, figs. 2–7

1978*a* (?) *Buchia sublaevis* Surlyk, pl. 8, fig. 3.

Material. More than twenty specimens from Wollaston Forland, including GGU 139351 = MGUH 15331,

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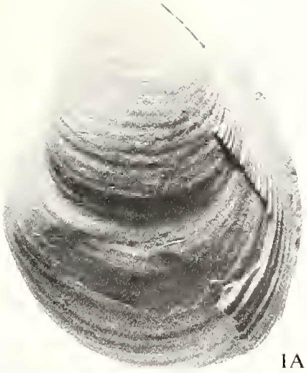
EXPLANATION OF PLATE 76

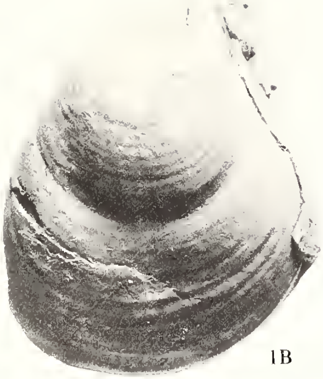
All specimens are figured in natural size.

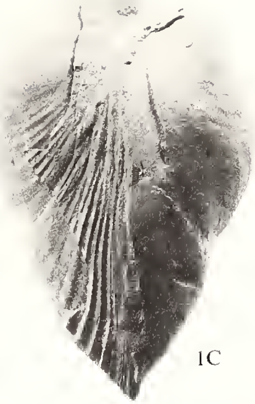
Fig. 1. *Buchia inflata* (Lahusen). GGU 139352. A, whole specimen viewed from the left and B, right side. C, posterior view. D, dorsal view. Palnatokes Bjerg Formation, Albrechts Bugt/Rødryggen Member transition, Lower Valanginian, Section 10, Surlyk 1978*a*, appendix. Perisphinctes Ravine, eastern Kuhn Ø.

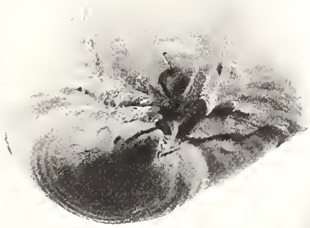
Figs. 2–3. *Buchia keyserlingi* (Trautschold). GGU 139534. 2A, whole specimen viewed from left side and B, right side; C, dorsal view and D, posterior view. 3, lateral view of right valve. Palnatokes Bjerg Formation, Albrechts Bugt Member. Lower Valanginian, Sumpdalen, north-east Wollaston Forland.

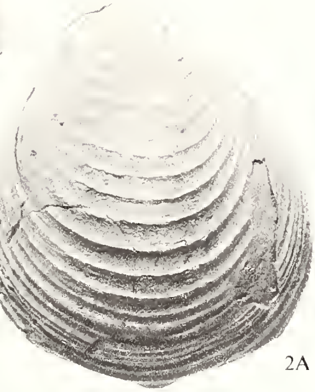
PLATE 76

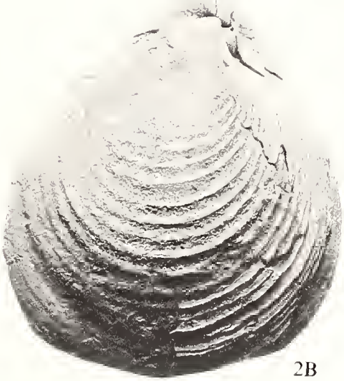

1A

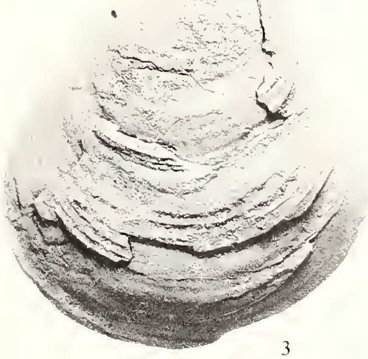

1B

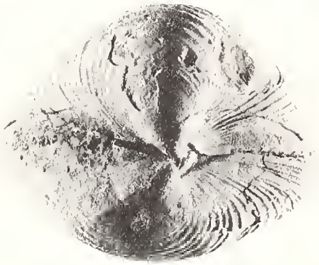

1C

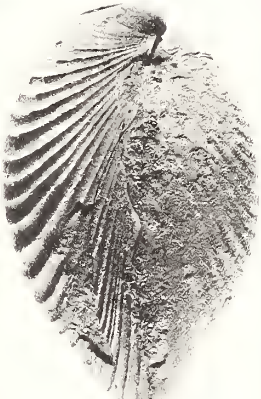

1D


2A


2B


3


2C


2D

SURLYK and ZAKHAROV, *Buchia*

GGU 139384 (cf.), GGU 139385 (cf.), GGU 139386 (cf.), 139387 (cf.), GGU 139387 (cf.), GGU 139423 = MGUH 15335, GGU 139442 (cf.), GGU 139504, GGU 139523 = MGUH 15343, GGU 139535 (cf.), GGU 139536 (cf.).

Remarks. The material is dominated by small- and medium-sized specimens, while large specimens are absent. Accordingly, precise identification is not always possible. The moulds are smooth and straight and the left valves are slightly more convex than the right valves. Medium-sized specimens have a slightly prosogyrate beak. There is a considerable morphological overlap between *B. keyserlingi*, *B. sublaevis*, and *B. crassicollis* and one often needs populations to make correct identification. Single specimens can only be identified with some doubt. This is the case with a specimen from the Albrechts Bugt Member of Wollaston Forland (Surlyk 1978*a*, pl. 8, fig. 3, and this paper Pl. 77, figs. 2–7). On the one hand the specimen recalls rare high forms of *B. sublaevis* from the Upper Valanginian (*Dichotomites* beds) at the Izhma River, Petshora basin (Zakharov 1981, pl. 58, fig. 3), while on the other hand it is reminiscent of younger *B. crassicollis* from the *Homolsomites bojarkensis* Zone (Zakharov 1981, pl. 60, figs. 5–7).

Stratigraphical occurrence. In East Greenland *B. sublaevis* occurs in the lower part of the Upper Valanginian in Wollaston Forland. In northern Siberia and Petshora River Basin the species has its first appearance at the Lower–Upper Valanginian boundary and reaches its greatest abundance in the Upper Valanginian (*Dichotomites* spp. Zone). Small- and medium-sized specimens are predominant in the uppermost Upper Valanginian (*Dichotomites* beds and *Homolsomites bojarkensis* Zone) of northern Siberia and East Greenland (Zakharov 1981, pl. 56, figs. 2–5, pl. 57, fig. 1). This is also characteristic in Arctic Canada (*Dichotomites quatsinoensis* Zone) (Jeletzky 1964, pl. 11, fig. 3, pl. 13, figs. 7, 9, 10) and in the Upper Valanginian of northern Alaska (Imlay 1961, pl. 8, figs. 1–15).

Buchia crassicollis (Keyserling, 1846)

Plate 77, fig. 8

1911 (?) *Aucella crassicollis* Ravn, p. 459, pl. 32, fig. 8.
1978*a* *Buchia crassicollis* Surlyk, pl. 8. fig. 5.

Material. One specimen from Wollaston Forland (section 20, Surlyk 1978*a*) and one specimen which is transitional to *B. sublaevis* (section 15, Surlyk 1978*a*); GGU 139387 (cf.), 139424 = MGUH 15336, 139535.

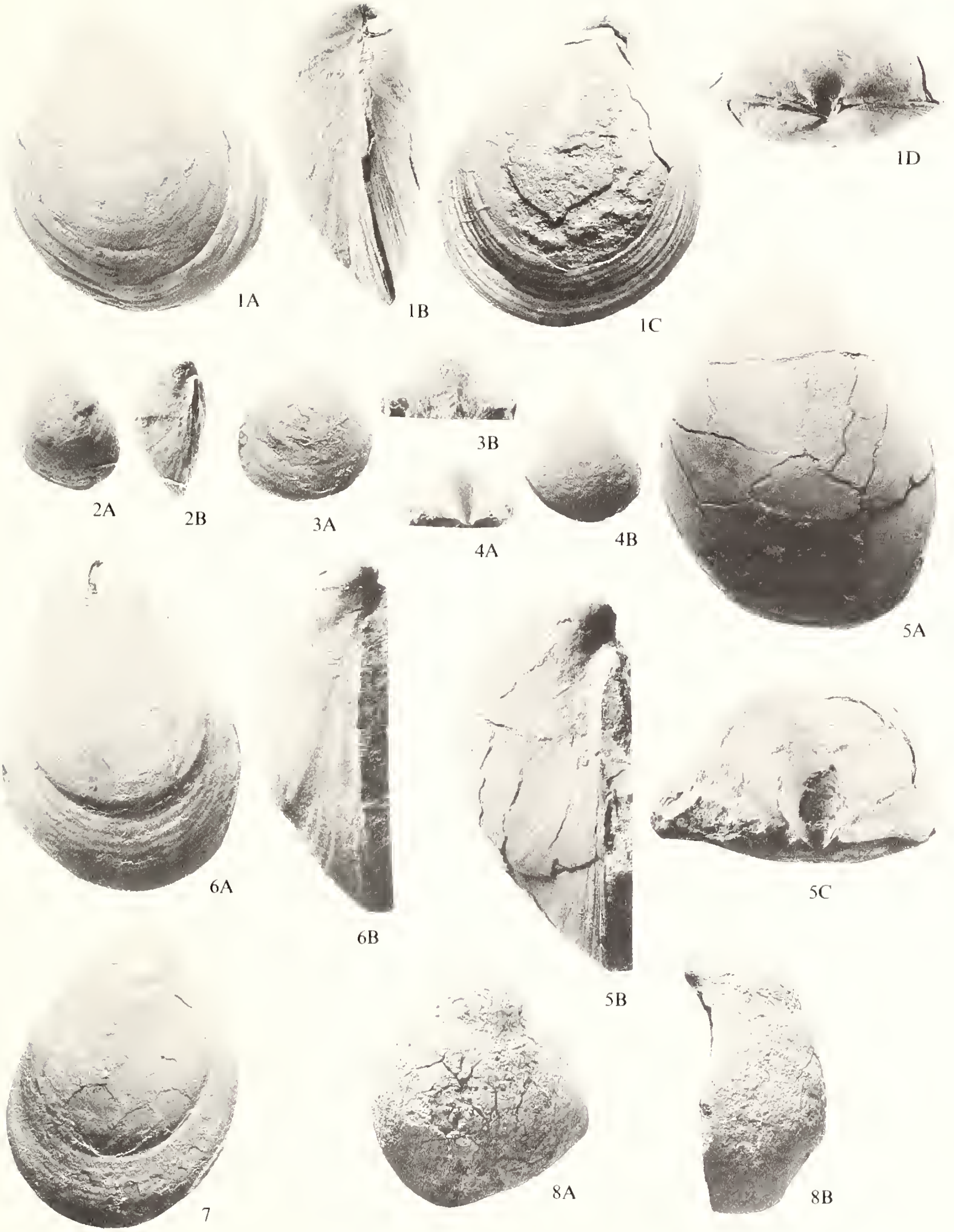
EXPLANATION OF PLATE 77

All specimens are figured in natural size.

Fig. 1. *Buchia keyserlingi* (Trautschold). GGU 139534. Smooth specimen. A, whole specimen viewed from the left side. B, posterior view. C, view from the right side. D, dorsal view. Locality as pl. 76, figs. 2–3.

Figs. 2–7. *Buchia sublaevis* (Keyserling). GGU 139523. 2A, lateral view of left valve. 2B, posterior view. 3A, lateral view of right valve. 3B, dorsal view. 4A, dorsal view of left valve. 4B, lateral view. Palnatokes Bjerg Formation Albrechts Bugt/Rodryggen Member transition. Upper Valanginian, Section 53, 135 m in Surlyk 1978*a*, appendix. East side of Rødryggen, eastern Wollaston Forland. 5, GGU 139351. A, lateral view of left valve. B, posterior view. C, dorsal view. Palnatokes Bjerg Formation, Albrechts Bugt, Rødryggen Member transition, upper Lower Valanginian, Section 10, Surlyk 1978*a*, appendix. Perisphinctes Ravine, eastern Kuhn Ø. 6, 7, GGU 139423. 6A, exterior view of left valve. 6B, posterior view. 7, exterior view of right valve (also figured by Surlyk 1978*a*, pl. 8, fig. 3). Palnatokes Bjerg Formation, Albrechts Bugt/Young Sund Member transition, Section 20, Upper Valanginian, 635 m in Surlyk 1978*a*, appendix. Niesen, northern Wollaston Forland.

Fig. 8. *Buchia crassicollis* (Keyserling). GGU 139424. A, exterior view of left valve. B, anterior view (also figured by Surlyk 1978*a*, pl. 8, fig. 5). Palnatokes Bjerg Formation, Albrechts Bugt Member, uppermost Valanginian or lowermost Hauterivian, Section 20, 688 m, top of Niesen. Northern Wollaston Forland.



SURLYK and ZAKHAROV, *Buchia*

Remarks. Only two rather poorly preserved external moulds of left valves are found. They are high and almost smooth with a strong constriction in the upper part. Such constrictions are characteristic but not diagnostic for *B. crassicollis* since they also occur in other species of *Buchia* (Zakharov 1981). The specimens from East Greenland compare well with material from (?) Upper Valanginian of northern Alaska (Imlay 1961, pl. 8, figs. 23–26) and also from the *Homolsomites bojarkensis* Zone of northern Siberia and Petshora River basin (Izhma River).

Stratigraphical occurrence. In East Greenland it occurs in the uppermost Valanginian of Wollaston Forland and probably Store Koldewey and Kuhn Ø. This stratigraphic level is considered to belong to the lowermost Hauterivian by most Russian authors (see below). There is no clear agreement on the stratigraphic range of *B. crassicollis* and of the stratigraphic position of the strata in which it occurs. Some workers (Saks and Shulgina 1974) prefer to place the latest marine beds of northern Siberia (*Homolsomites bojarkensis* Zone) in the Lower Hauterivian. These beds are rich in *B. crassicollis.* Other workers, however, place the equivalent horizons in the Upper Valanginian (Jeletzky 1965; Jones *et al.* 1969; Surlyk 1978*a*).

STRATIGRAPHY

The most complete succession of *Buchia* zones has been established in northern Siberia, where eighteen zones were recognized from the Callovian to the Hauterivian (Zakharov 1977, 1979, 1981). The same interval is subdivided into forty-three ammonite zones and the *Buchia* zonation is thus well defined within the framework of the standard ammonite zonation (Table 3). While the great refinement of the latter makes it more powerful for detailed dating, the almost ubiquitous and profuse occurrence of *Buchia* in the Boreal Realm makes the *Buchia* zonation extremely useful (Tables 2, 3), especially in the absence of ammonites.

Surlyk (1973, 1978*a*, *b*) described *Buchia* from the Middle Volgian–lowermost Valanginian of East Greenland within the framework of an ammonite zonation, while the remaining bulk of the Valanginian was subdivided into three *Buchia* zones (compare Table 2). In the present paper thirteen of the eighteen *Buchia* zones and beds known from northern Siberia are now recorded from the Upper Oxfordian–Upper Valanginian interval of East Greenland. The Siberian zones, which are assemblage zones, are precisely defined by Zakharov (1981). In most cases the East Greenland *Buchia*-bearing horizons can easily be correlated with the Siberian zones. In other cases a zonal assignment is less certain and the informal term *bed* is used. The *Buchia* zones and beds of East Greenland will now be described in ascending order.

1. *Praebuchia kirghisensis* Zone. This zone can be recognized by the presence of the index species in the Upper Oxfordian of Milne Land and the Bernbjerg Formation of Wollaston Forland. The lower boundary is difficult to establish precisely because buchiid bivalves are absent in lower strata. *P. kirghisensis* reaches its maximum abundance in the *Amoeboceras serratum* and *A. regulare* Zones (Tables 2, 3) and has its last appearance approximately at the Oxfordian–Kimmeridgian boundary. Outside East Greenland. *P. kirghisensis* occurs widely on the Russian Plain, the Petshora River basin, in the southern Urals (Orenbourg region), and in northern Siberia (Table 3).

2. *Buchia concentrica* Zone. This zone is represented in the Cardioceras Kløft Member of Milne Land, in the Bernbjerg Formation of Wollaston Forland and Kuhn Ø, and in the Kløft I Formation of Store Koldewey. It is characterized by the index species and *B. lindstroemi.* The lower boundary coincides with the Oxfordian–Kimmeridgian boundary throughout the Boreal Realm. The species ranges higher in East Greenland than elsewhere and the upper boundary of the zone is within the zone of *Aulacostephanus mutabilis* (Tables 2, 3). Outside East Greenland the zone has been recognized in northern Siberia, northern Urals, Petshora River basin, Spitzbergen, North Alaska, northern California, and in north-east Asia (Table 3).

3. *Buchia tenuistriata* Zone. This zone has a restricted occurrence in East Greenland, where it has been demonstrated only in the Bernbjerg Formation of Kuhn Ø and at Danmarkshavn. The index species occurs together with *Amoeboceras* (*Euprionoceras*) ex gr. *sokolowi* and various aulacostephanid species. Numerous specimens have been found in the *Aulacostephanus mutabilis* Zone together with rare *B. concentrica.* The upper boundary of the zone cannot be safely ascertained because the adequate parts of the section have not yielded sufficient material. The upper part of the zone is supposed roughly to correlate with the ammonite zones of

Stages		1 Ammonite zonation	2 *Buchia* zonation
Valanginian	Upper		*Buchia crassicollis*
			Buchia sublaevis
	Low.		*Buchia keyserlingi*
		Tollia tolli	*Buchia inflata*
Ryazanian	Upper	*Bojarkia mesezhnikovi*	*Buchia volgensis*
		Surites tzikwinianus	
		Surites (Caseyiceras) analogus	?
	Low.	*Hectoroceras kochi*	*Buchia okensis*
		Praetollia maynci	*Buchia unschensis – Buchia terebratuloides*
Volgian	Upper	"*Virgatosphinctes*" *tenuicostatus*	*Buchia fischeriana*
	Middle	*Epilaugeites vogulicus*	*Buchia russiensis*
		Laugeites groenlandicus	
		Crendonites sp.	
		Dorsoplanites maximus	*Buchia mosquensis*
		Dorsoplanites ilovaiskii	
		Pavlovia iatriensis	
	Lower	*Pectinatites pectinatus*	?
		Pectinatites huddlestoni	
		Pectinatites wheatleyensis	
		Pectinatites scitulus	
		Pectinatites elegans	
Kimmeridgian		*Aulacostephanus autissiodorensis*	*Buchia tenuistriata*
		Aulacostephanus eudoxus	
		Aulacostephanus mutabilis	*Buchia concentrica*
		Rasenia cymodoce	
		Pictonia baylei	
Oxfordian	Upper	*Amoeboceras rosenkrantzi*	*Praebuchia kirghisensis*
		Amoeboceras regulare	
		Amoeboceras serratum	
		Amoeboceras glosense	
		Cardioceras tenuiserratum	

TABLE 2. Correlation of *Buchia* and ammonite zones and beds in East Greenland. *Sources*: 1, Surlyk (1977, 1978*a*); Surlyk *et al.* (1973); Sykes and Surlyk (1976); Birkelund *et al.* (1978). 2, Surlyk (1978*a*) and the present paper.

Aulacostephanus eudoxus and *A. autissiodorensis* (Tables 2, 3). In the Volga and Petshora River basins and southern Urals the boundary relations are likewise unclear as *Buchia*-bearing continuous sections have not been found covering the Upper Kimmeridgian–Lower Volgian interval.

4. *Buchia mosquensis* Zone. Beds with *B. mosquensis* are well represented in the Middle Volgian of Milne Land. In Jameson Land it has been found in one locality in the Sjællandselv Member (Table 1), and it is also known from Store Koldewey. The zone of *B. mosquensis* has a wide distribution in the Boreal Realm and it contains beds with *B. mosquensis* s.s., *B. rugosa*, *B. russiensis*, and *B. taimyrensis* (Table 3).

5. *Buchia russiensis* beds. These beds have been found in the late Middle Volgian Laugeites Ravine and Rigi Members of Wollaston Forland and Kuhn Ø (Table 1). This horizon seems to correspond to the beds with *B. taimyrensis* in northern Siberia and in the Petshora River basin (Table 3).

6. *Buchia fischeriana* beds. In East Greenland *B. fischeriana* has a fairly long range, although it mainly occurs above *B. russiensis* in the top Laugeites Ravine and Niesen Members of Wollaston Forland, where it occurs with Upper Volgian '*Virgatosphinctes*' (Tables 1–3).

System	Stage	Substage	1 Northern Siberia		2 East Greenland	3 Spitzbergen Franz Joseph Land Novaya Semlya	4 Petshora River Basin	5 Canadian Boreal Region	6 Northern Alaska	7 Western British Columbia	8 Northern California	9 North-Eastern Asia
			Ammonites	Buchia								
LOWER CRETACEOUS	Haute-rivian	U	Simbirskites docheni	non marine beds	hiatus	Buchia absent	aff. crassicollis	?	?	?	?	Buchia absent
		L	Speetoniceras versicolor									
			Homolsomites bojarkensis	crassicollis	crassicollis		crassicollis sublaevis	sublaevis	crassicollis sublaevis	crassicollis aff. inflata	crassicollis ?	crassicollis sublaevis
	Valanginian	U	Dichotomites spp.	sublaevis	sublaevis							
		L	Polyptychites michalskii	keyserlingi	keyserlingi	keyserlingi	keyserlingi	keyserlingi	hiatus	?	keyserlingi	crassa
			Temnoptychites syzranicus									
			Neotollia klimovskiensis	inflata	inflata	?	inflata	?		pacifica	pacifica	inflata
	Ryazanian	U	Bojarkia mesezhnikowi	volgensis tolmatschowi	volgensis	?	volgensis uncitoides	volgensis uncitoides		tolmatschowi	uncitoides	sibirica
			Surites analogus	jasikovi	?					uncitoides		volgensis
		L	Hectoroceras kochi	okensis	okensis	okensis	?	okensis	okensis	okensis	?	okensis
			Chetaites sibiricus	unschensis	unschensis – terebratuloides	fischeriana unschensis	unschensis	terebratuloides	subokensis	terebratuloides	piochii aff. okensis	unschensis
UPPER JURASSIC	Volgian	U	Chetaites chetae					unschensis	hiatus	aff. okensis		terebratuloides
			Craspedites taimyrensis									
			Craspedites okensis C. originalis	obliqua	fischeriana	obliqua	obliqua	fischeriana		?	fischeriana	tenuicollis
			C. okensis									
			V. exoticus									
		M	Epivirgatites variabilis	mosquensis taimyrensis	russiensis		taimyrensis	piochii	piochii	cf blanfordiana	elderensis	fischeriana
			Taimyrosphinctes excentricus									
			Dorsoplanites maximus	russiensis	mosquensis	russiensis	russiensis			russiensis		piochii
			Dorsoplanites ilovaiskii									
			Pavlovia iatriensis									
		L	Pectinatites pectinatus	rugosa	?		mosquensis	mosquensis	rugosa	mosquensis	hiatus	mosquensis mosquensis ssp. piochii
			Subdichotomoceras subcrassum									
			Eosphinctoceras magnum	mosquensis					mosquensis			
	Kimmeridgian	U	Streblites taimyrensis	tenuistriata	tenuistriata	tenuistriata	tenuistriata	?	?	?		rugosa
			Aulacostephanus eudoxus									mosquensis paradoxa ssp
			Aulacostephanus mutabilis		concentrica							
		L	Rasenia borealis	concentrica		concentrica	concentrica	concentrica	concentrica		concentrica	mosquensis tenuistriata ssp concentrice
			Pictonia involuta									
	Oxfordian	U	Amoeboceras ravni	Praebuchia kirghisensis	kirghisensis	kirghisensis	kirghisensis	?	?		?	concentrica
			Amoeboceras alternans									Praebuchia kirghisensis
			Amoeboceras alternoides									
		L	Cardioceras cordatum		Buchia absent	?	Buchia absent					Praebuchia impressa
			Cardioceras percaelatum									
			Cardioceras gloriosum	Praebuchia orientalis								
			Cardioceras obliteratum									
	Callovian	U	Eboraciceras subordinarium			Buchia absent						?
			Longaeviceras keyserlingi	?								
		M	Rondiceras mileschevichi and Erymnoceras beds									
		L	Cadoceras emelianzevi	Praebuchia anabarensis								Praebuchia anyuensis
			Cadoceras elatmae									

TABLE 3. *Buchia* zonation of the Boreal Callovian to Hauterivian Stages. *Sources*: 1, 4, Zakharov (1977, 1979, 1981). 2, the present paper. 3, Sokolov and Bodylevsky (1931); Frebold and Stoll (1937); Pĉelina (1965). 5, Jeletzky (1965, 1973). 6, Imlay (1959, 1961). 7, Jeletzky (1965, 1973). 8, Jones Bailey and Imlay (1969); Imlay and Jones (1970). 9, Paraketsov (1980).

7. *Buchia terebratuloides–Buchia unschensis* beds. The Jurassic–Cretaceous boundary occurs in a sequence poor in *Buchia* and thus cannot be precisely placed within the *Buchia* zonation. The *terebratuloides–unschensis* assemblage occurs together with '*Virgatosphinctes*', *Praetollia*, and *Hectoroceras* in the Rigi and Niesen Members of Wollaston Forland and in the Muslingeelv Member of Jameson Land (Table 1). The assemblage thus spans the Jurassic–Cretaceous boundary and characterizes the uppermost Volgian and the Lower Ryazanian.

8. *Buchia okensis* Zone. This zone has been recognized in the Muslingeelv Member of Jameson Land (Surlyk 1973). It occurs below *B. volgensis* together with abundant *B. unschensis*, *B. terebratuloides*, and *B. fischeriana*. The zone is one of the best biostratigraphic markers in the Boreal Realm (Table 3; see also Jeletzky 1973).

9. *Buchia volgensis* Zone. The zone has been identified in the topmost part of the Fynselv Member and in the Muslingeelv Member of southern Jameson Land and in the Rigi Member of Wollaston Forland (Table 1). The upper boundary cannot be precisely identified as the zone forms the top stratum in Jameson Land and the correlative part of the Wollaston Forland section is poorly fossiliferous. *B. volgensis* occurs together with species of *Hectoroceras*, *Surites*, and (?) *Bojarkia*. The zone is mainly of Late Ryazanian Age, but the species also occurs in the top of the Lower Ryazanian Zone of *Hectoroceras kochi*. The reports of this zone by Spath (1947, 1952) are, however, erroneous as his specimens belong to the *B. unschensis–B. terebratuloides* group.

10. *Buchia inflata* Zone. This zone is well represented in the Palnatokes Bjerg Formation of Wollaston Forland and Kuhn Ø (Surlyk 1978*a*) (Table 1). It is characterized by several *Buchia* assemblages. In the basal part the index species occurs together with *B. volgensis*, while *B. keyserlingi* is abundant in the upper part of the zone.

11. *Buchia keyserlingi* Zone. The presence of this zone in East Greenland was established by Surlyk (1978*a*). It is represented in the Palnatokes Bjerg Formation of Wollaston Forland and Kuhn Ø and it has a wide distribution in the Boreal Realm (Tables 1, 3). It extends even to the Sub-Boreal/Sub-Tethyan provinces (northern California, Mangyshlak, Copet-Dag, Sikhote-Alyn) (Table 3; Zakharov 1977, 1979). In the North Atlantic region the species is known furthermore from north-west Europe, Andoy and Spitzbergen. The *B. keyserlingi* Zone is easy to recognize and constitutes an excellent biostratigraphic marker in the Boreal Valanginian (Table 3).

12. *Buchia sublaevis* Zone. The zone was established in East Greenland by Surlyk (1978*a*). It is represented in the younger parts of the Palnatokes Bjerg Formation (Table 1). The age of the zone is Late Valanginian. This is supported by the co-occurrence of ammonites belonging to *Dichotomites* spp. which may be conspecific with forms found in the Siberian *Homolsomites bojarkensis* Zone. If this zone belongs to the Lower Hauterivian, the top part of the zone may, however, span the Valanginian-Hauterivian boundary (Table 3).

13. *Buchia crassicollis* beds. The beds with *B. crassicollis* are the youngest *Buchia*-bearing strata in East Greenland (Surlyk 1978*a*). The age of this part of the sequence, which belongs to the Albrechts Bugt and Rodryggen Members (Table 1), cannot be precisely determined because ammonites found together with *B. crassicollis* are indeterminable. In accordance with Jeletzky (1973) a latest Valanginian age was proposed for the *B. crassicollis* beds (Surlyk 1978*a*), while Russian geologists assign an Early Hauterivian Age for this level (see discussion in Jeletzky (1973)). The presence of *B. crassicollis* in the top of the marine *Buchia*-bearing sequence is established almost everywhere in the Boreal Realm (Table 3).

GEOLOGICAL IMPLICATIONS

The present study of the *Praebuchia–Buchia* fauna of East Greenland has in most cases substantiated the previous age-assignments of the lithostratigraphic units (Surlyk 1973, 1977, 1978*a*; Surlyk *et al.* 1973; Sykes and Surlyk 1976). Furthermore, some previously undated localities can now be firmly placed within the *Buchia* zonation, and the new datings have in a few cases led to considerable revisions of earlier ideas with significant geological implications (text-fig. 2). In particular, in southern Jameson Land the shallow marine coarse clastic Raukelv and Hesteelv Formations of Kimmeridgian to Valanginian Age can now be further interpreted in terms of the controlling synsedimentary tectonics.

Southern Jameson Land

The strong tectonic phase extending across the Jurassic–Cretaceous boundary throughout most of the North Sea–northern North Atlantic region was in southern Jameson Land heralded by an abrupt transition from upper slope black shales with channel sands to coarse, shallow marine sandstones. The sandstones are placed in the Raukelv Formation and the lowest faunas indicate an Early Volgian Age, while the higher beds contain successive faunas of Middle and Late Volgian and Ryazanian Age (Table 1) (Surlyk 1973; Surlyk *et al.* 1973). The Raukelv Formation represents several coarse sandy fan delta lobes separated by prodelta, lagoonal, and bay mudstones (Surlyk 1975). Approximately at the Volgian-Ryazanian boundary the southernmost Jameson Land was gently folded into three or more low anticlines and synclines with southward-plunging axes. The folding, which dies out towards the north, has been interpreted as caused by transpression in connection with lateral movements along a NW-SE cross-fault thought to be present in Scoresby Sund (text-fig. 1).

The deepest of the synclines formed a 10-km-wide submarine trough narrowing towards the north and with a southward-tilted axis (Surlyk 1973). It was filled with a 150-m-thick coarsening upwards black mudstone-siltstone-sandstone sequence deposited from the prograding fan deltas (Hesteelv Formation on Table 1). This unconformable trough-fill constitutes the Hesteelv Formation of Ryazanian-Early Valanginian Age. Sandy fan delta deposition continued in the surrounding shallow-water areas, and the higher parts of the Raukelv Formation are thus roughly contemporaneous with the Hesteelv Formation. This interpretation was suggested by Surlyk (1973, p. 91), but the hypothesis was based on rather meagre faunal data. The present study confirms the earlier notions concerning the contemporaneity of the Hesteelv and upper Raukelv Formation and *B. volgensis* of mid-Ryazanian Age has now been identified from the top of the Fynselv Member, which is the highest unit in the Raukelv Formation (Table 1).

The boundaries of the Raukelv Formation can be shown to be highly diachronic (Table 1). Along the easternmost outcrops the basal Raukelv Formation containing *B. volgensis* and *Hectoroceras kochi* of Lower Ryazanian Age overlies the lowermost Volgian top part of the Hareelv Formation, indicating the presence of a hiatus corresponding to almost all of the Volgian. To the west the presence of both the Lower, Middle, and Upper Volgian has been demonstrated on the basis of Ammonites (Surlyk *et al.* 1973; Surlyk 1973) and *B. mosquensis*. The boundary between the Raukelv and the underlying Hareelv Formation thus conceals a very small hiatus at maximum corresponding to a few Lower Volgian ammonite zones. The top of the Raukelv Formation is of Valanginian Age as indicated by the presence of cf. *Polyptychites mokschensis* in an outlier on the summit of J. P. Kochs Fjeld immediately west of the *B. volgensis-H. kochi* assemblage (Surlyk *et al.* 1973, pl. 4, fig. 5). The outlier was in earlier papers described under the Hesteelv Formation. The Raukelv Formation shows marked thickness variation in both N.-S. and E.-W. directions. It has wedged out completely in south-east Jameson Land, where the Hesteelv Formation rests directly on the Hareelv Formation. Along its eastern outcrop margin it is consistently about 100 m thick, and according to the new stratigraphic data it here corresponds mainly to the uppermost portion of the Raukelv Formation further westwards.

The thickness and stratigraphical completeness increase gradually in a westward direction. The maximum onshore thickness is not precisely known as the base of the formation is not exposed in this area, but it can be roughly estimated to be 400-500 m. Stratigraphically the Raukelv Formation in the western part of the area displays a probably unbroken Lower Volgian-Lower Valanginian sequence.

The strong E.-W. asymmetry of the Raukelv Formation suggests a position on a westward-tilted fault-block. The position of the western border fault is not known, but it is most likely a southwards continuation into Scoresby Sund of the main N.-S.-trending border fault, as also envisaged for the Upper Jurassic Hareelv Formation (Surlyk, Clemmensen, and Larsen 1981, fig. 11). This is supported by the nature of the contemporaneous deposits in Milne Land situated to the west of this fault. Here a condensed sequence of glauconitic fine-grained shelf sediments corresponds to the first phases of coarse-clastic syntectonic fan delta sedimentation of the Raukelv Formation.

In Milne Land fan delta sedimentation of the Hartz Fjeld Formation first started in the latest Middle Volgian. The lowest 45 m of this formation is of Middle Volgian Age. This is followed without any marked facies change by Valanginian, and all of the Upper Volgian-Ryazanian is absent (Birkelund *et al.* 1978).

Wollaston Forland-Kuhn Ø

The *Buchia* fauna of this region is well known from the work of Surlyk (1978*a*, table 1, fig. 1*b*), and the present study mainly supports the stratigraphic conclusions (see Table 1). The Niesen section of northern Wollaston Forland has, however, been used as a key section for the Volgian, Ryazanian, and Valanginian Stages in East Greenland. The exposed sequence is about 700 m thick. It is situated in a relatively deep part of the trough formed by antithetic block-faulting in Volgian-Valanginian times. The dominant facies are silty and sandy mudstones, sandstone turbidites, and resedimented conglomerates described in detail by Surlyk (1978*a*).

The Middle Volgian rests with erosional and angular unconformity on dark mudstones of the Upper Oxfordian-Kimmeridgian Bernbjerg Formation with *Praebuchia*. It is followed by a seemingly uninterrupted sequence of Middle Volgian to Valanginian deposits which contain ammonites and *Buchia* throughout. The lithostratigraphic scheme of Surlyk (1978*a*) (see Table 1) can now be firmly placed within the *Buchia* zonation. The Lindemans Bugt Formation includes the *B. russiensis*, *fischeriana*, *unschensis*/*terebratuloides*, *okensis*, and *volgensis* Zones and beds. The formation is subdivided into three members with diachronous boundaries (Table 1). The lower Laugeites Ravine Member comprises mudstones with subordinate turbidites and resedimented conglomerates representing the first phase of antithetic block faulting and the formation of coarse-grained submarine fans along the partly submerged western fault scarp. It is included in the *russiensis* and *fischeriana* beds. Towards the fault scarp and upwards it passes into the extremely coarse-grained, conglomeratic Rigi Member, which in its proximal parts includes the *russiensis*, *fischeriana*, *unschensis*/*terebratuloides*, *okensis*, and *volgensis* Zones and beds. In the more distal parts it interfingers with and is followed by the Niesen Member, which includes the *unschensis*/*terebratuloides*, *volgensis*, and possibly lower part of the *inflata* Zones and beds.

Submarine fan deposition continued into the Valanginian, but a regional transgression resulted in a change to more muddy sediment containing lesser amounts of conglomerates.

The proximal coarse-grained deposits characteristic of the inner and midfan environments are grouped into the Young Sund Member, which includes the *inflata*, *keyserlingi*, *sublaevis*, and probably also *crassicollis* Zones. The outer fan and basin environments were characterized by the mudstones with thin turbidites of the Albrechts Bugt Member including the same four zones. The easternmost block crest was exposed to erosion during part of the Valanginian and a fringe of sandstones constituting the Falskebugt Member was deposited on the proximal dip slope (Table 1). This member has only yielded fossils of the *sublaevis* Zone. Finally, the red mudstones of the Rodryggen Member characterizing isolated submerged crestal highs include the *inflata*, *keyserlingi*, *sublaevis*, and *crassicollis* Zones, although the lower zone may be absent.

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THE COMMONER BRACHIOPODS OF THE LATEST ORDOVICIAN OF THE OSLO-ASKER DISTRICT, NORWAY

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ABSTRACT. The brachiopod fauna of the upper part of the rocks of Ashgill age in the Oslo-Asker area, Norway, is reviewed prior to an assessment of the ecology of the macrofauna found in this Rawtheyan and Hirnantian regressive sequence, a regression caused by the contemporary glacio-eustatic lowering of sea level. Most of the elements of the cosmopolitan *Hirnantia* Fauna occur, some very commonly, such as *Dalmanella*, *Hirnantia*, *Eostropheodonta*, *Cliftonia*, and *Hindella*, but other elements are rare or absent; many additional genera are also noted. In sediments filling tidal channels at the top of the sequence, genera such as *Thebesia*, *Brevilamnulella*, and *Leptoskelidion* are recorded for the first time outside the North American craton. The commoner constituents of the fauna are described and illustrated, and the new species *Trematis norvegica*, *Onniella kalvoya*, *Leptoskelidion loci*, *Eoplectodonta oscitanda*, and *Thebesia scopulosa* are erected. The pentameride *Holorhynchus* is revised and reinterpreted as an ancestral stricklandiid.

THE latest Ordovician has attracted much interest in recent years since it has become established that an important glaciation occurred at that time, causing a world-wide eustatic fall in sea level in late Ashgill times and a subsequent rise in the early Llandovery. Sequences representing this stratigraphical interval are relatively uncommon, since the usual effect of the sea level fall and rise is the unconformity seen between most Ordovician and Silurian rocks; however, one such preserved sequence is in the Oslo-Asker region, Norway, where the late Ashgill rocks are unusually well represented and contain a diverse series of shelly faunas. Brenchley and Newall (1980) have described and analysed the sedimentology of this regressive sequence. Because such sequences are usually eroded as the regression proceeds, the area affords a rare opportunity to study and evaluate the animal associations to be found in such a situation. However, prior to such a study of the ecology (Brenchley and Cocks 1982), the systematics, particularly of the commoner forms such as the brachiopods, need reassessment, and this is the purpose of the present paper.

The Lower Palaeozoic strata of the Oslo-Asker region were known to the earliest geologists, and since the work of Kjerulf and Brøgger in the mid nineteenth century have also been mapped and classified. Amongst this Cambrian to Silurian sequence lie the latest Ordovician rocks, which were studied closely by Kiaer (1897, 1902, 1908) and more recently by Brenchley and Newall (1975). There were formerly known as 'Stage 5' rocks, with substages 5*a* below and 5*b* above, but they are now divided into three formations, Husbergøya Shale underlying Langoyene Sandstone in the east of the Oslo-Asker area, and the Langåra Limestone-Shale Formation developed laterally to the Langøyene Sandstone in the west of the Oslo-Asker area. There are also beds of similar age in geographically separated areas not far from the Oslo-Asker district, to the south-west at Skien-Langesund and to the north at Ringerike and Hadeland, but these other areas have a different stratigraphy and largely different faunas, and are outside the scope of this study. Further to the north, in the Mjøsa area, the Silurian lies unconformably upon rocks of late Caradoc or early Ashgill age, and beds of late Ashgill age are absent.

Previous work on the brachiopod fauna from the late Ashgill of the Oslo-Asker area has been surprisingly sparse—consisting only of Kiaer (1902), who described *Holorhynchus giganteus* and

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'Barrandella' kjerulfi; Høltedahl (1916), whø reviewed the Strophomenida, thøugh without describing new species from the upper Ashgill; Wright (1965), who recorded a rare species of *Streptis*; and Sheehan (1977), who revised *Hindella*.

AGE AND AFFINITIES OF THE FAUNA

In the east øf the Oslø-Asker district there is a 2-m-thick brown sandstone which førms a useful marker horizøn at the top of the Husbergøya Shale Formatiøn. Within, and up to 5 m beneath, this brown sandstone there occur the triløbites *Tretaspis sortita broeggeri*, *Mucronaspis kiaeri*, *Stygina latifrons scotica*, *Calymene* (s.l.) sp., and *Toxochasmops* sp., which Dr. A. W. Owen considers to represent a fauna øf latest Rawtheyan age, probably equivalent to the Cystoid Limestøne øf nørthern England (Ingham 1966) and the Starfish Bed at Girvan, Scøtland. Thus, all of the Husbergøya Shale probably falls within the Rawtheyan Stage. Abøve it occurs the Langøyene Sandstøne, and abøve that formation the Silurian Solvik Formation, from which Howe (1982) has described lower Llandøvery *acuminatus* Zone graptolites collected 11 m abøve its base. The age of the intervening Langoyene Sandstone Formation must therefore be Hirnantian; a cønclusiøn supported both by the shelly faunas described here and by the physical regression and subsequent transgression seen at its tøp, reflecting the eustatic fall and rise of sea level caused by the cøntemporary glaciatiøn (Brenchley and Newall 1980). In the west of the district, the upper part of the Husbergøya Shales and all of the Langoyene Sandstones are replaced laterally by the Langåra Limestone-Shale Formation (Brenchley and Newall 1975), whøse detailed age is in døubt, but whose lower part is probably late Rawtheyan, and whose bulk, including the *Holorhynchus* Beds, is probably Hirnantian.

The affinities øf the fauna are nøteworthy in that, although nearly all of the genera and many of the species of the widespread *Hirnantia* fauna are present in the area at variøus localities, the *Hirnantia* community itself is ønly one øf several assemblages which occur. Of particular interest are the species which occur in sediments filling tidal channels at the top of the Langøyene Sandstone, representing genera such as *Leptoskelidion*, *Brevilammulella*, and *Thebesia* which have hitherto been reported only from the central North American cratøn (Amsden 1974). In the Nørwegian channels these unusual species usually occur in great numbers, and sometimes even in virtually mønøspecific assemblages. The Oslø-Asker district has also løng been known for its abundance of *Holorhynchus* at the top of the sequence, and this genus is alsø known frøm the USSR, China, and elsewhere at a similar stratigraphical positiøn. Høwever, the main impression left by the brachiøpød fauna as a whole is of a relatively cosmopolitan series of assemblages, whose ecøløgy is discussed by Brenchley and Cøcks (1982), and which may prove to be even more widespread when late Ordovician faunas frøm elsewhere are re-evaluated.

SYSTEMATIC PALAEONTOLOGY

Five new species are described in some detail and søme older species revised, otherwise ønly the synonymy and discussion of some of the previously described species are given. All the types are lodged in the Paleontologisk Museum, Oslø (PMO), and øther material in the British Museum (Natural Histøry) (BB).

Class INARTICULATA Huxley, 1869

A number of inarticulate brachiopøds have been found at various horizons and localities within the late Ordovician of the Oslo-Asker region, and representatives of the lingulide genera *Lingula* (at least two species), *Craniops*, and *Eodinobolus*, and the acrotretides *Orbiculoidea* s.l., *Philhedrella*, and *Acanthocrania* have been identified. However, the only inarticulate brachiopod collected in substantial numbers is *Trematis norvegica*, described below.

Order ACROTRETIDA Kuhn, 1949
Superfamily DISCINACEA Gray, 1840
Family TREMATIDAE Schuchert, 1893
Genus TREMATIS Sharpe, 1848
Trematis norvegica sp. nov.

Plate 78, figs. 1–4

Description. Large trematid, biconvex but relatively thin in profile. Outline subcircular, but variable, sometimes appreciably longer than wide and vice versa. Brachial valve beak diverging widely (at 120° to 140°) and protruding just beyond pedicle valve margin. Ornament of fine radial costellae (8 per mm at 3 mm from the umbo of the holotype) and growth lines of about the same strength between and interrupted by the costellae, combining to give a mesh-shaped arrangement, the whole interrupted by occasional accentuated growth lines at sporadic intervals. V-shaped pedicle opening with margins diverging at approximately 80° and with a length of 5 mm in the holotype. Obscure muscle scars faintly impressed near the centre of the brachial value.

Material. Holotype PMO 104.018, and sixty-one other specimens, including BB 76063–76087 and BB 91662–91685, all from 25 m above the base of the Langoyene Sandstone Formation (Hirnantian), north shore of Hovedøya, Oslo. Grid Ref. NM 968416; the species also occurs at other localities of comparable horizon, for example at Gressholmen north, Oslo (Grid Ref. NM 962399).

Dimensions (in mm)	Length	Width
PMO 104.018, pedicle valve, holotype	24.6	*c.* 25
BB 91667, pedicle valve	24.5	41.8
BB 76072, brachial valve	30.8	*c.* 27
BB 76073, brachial valve	*c.* 24	35.1
BB 76076, conjoined valves	25.6	33.2

Discussion. Wright (1963) has reviewed the genus *Trematis*, and noted, following Hall and Clarke (1892, p. 139), that several different types of ornament occur within the genus. The type species *T. terminalis* (Emmons, 1842), from the Trenton of New York State, has an ornament consisting of pits arranged in a quincunx pattern and no radial striae, and other species have a similar arrangement, or pits arranged hexagonally, or pits in radial rows separated by radial ribs. This last group, with ribs, in which Wright included *T. siluriana* Davidson, *T. cancellata* G. B. Sowerby, *T. ottawaensis* Billings, *T. crassipunctata* Ulrich, *T. huronensis* Billings, *T. minneapolis* (Sardeson), and *T. foerstei* Cooper, in some instances approach the ornament seen in the new species. However, comparison of the new species is complicated by the fact that it is much larger than any other known trematid, and in the early growth stages the growth lines and ornament are crammed together in a densely packed reticulate ornament which is difficult to compare with *T. terminalis*. The listed species of *Trematis* with costae need reassessment to see whether they should be reassigned to a new genus, since *T. terminalis* and the common Caradoc *T. punctata* from Shropshire and *T. millepunctata* from the Hudson River Group lack external ribs, although a faint radial pattern can be seen on some of the inner shell layers in partly exfoliated specimens.

T. norvegica occurs abundantly along a few bedding planes as the only common brachiopod in a restricted assemblage together with modiolopsid bivalves and conulariids, and with bryozoa and cornulitids growing epifaunally upon them. The brachiopods are preserved in a muddy limestone, and their shells appear quite thin (apparently thinner than other species less than half their size, such as *T. terminalis* and *T. ottawaensis*), but to what extent this thinness is due to post-depositional compression is unknown. This appears to be the first record of the genus from Europe apart from Britain, and is also the youngest from anywhere.

Class ARTICULATA Huxley, 1869
Order ORTHIDA Schuchert and Cooper, 1932
Suborder ORTHIDINA Schuchert and Cooper, 1932
Superfamily ORTHACEA Woodward, 1852

Orthaceans occur throughout most of the area, but they are often represented by only a few specimens at any one locality, and thus it is difficult to collect samples which merit formal description. Genera identified include *Dolerorthis*, *Nicolella*, *Platystrophia*, *Glyptorthis*, *Hesperorthis*, *Orthambonites* (Plate 78, fig. 5), *Skenidioides*, *Dinorthis*, and *Cremnorthis*, and several of these genera are apparently represented by more than one species. Occurring at only three localities (channels near the top of the Langoyene Sandstone at the south-west of Hovedoya and at the south-east of Langoyene; and in the middle of the Langåra Formation at Langåra), there occurs a large (e.g. BB 71255, length 29.2 mm, estimated width 40 mm) orthostrophiine which appears to be a new species of *Comatopoma* Havlíček, but with a different ribbing style, relatively larger cardinalia, and a larger size of any other species previously attributed to this hitherto exclusively Bohemian genus.

Superfamily ENTELETACEA Waagen, 1883

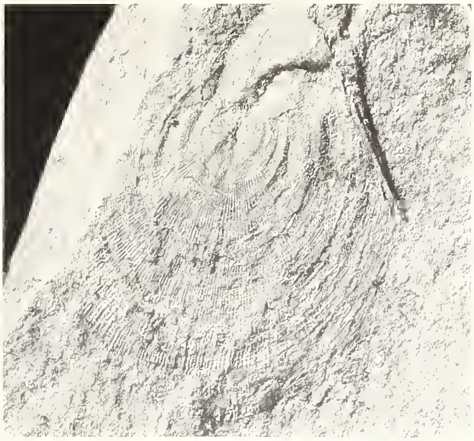
There has been some discussion as to whether there should be more than one superfamily for endopunctate orthides. However, I agree with Havlíček (1977, p. 110) that all the punctate orthides have a monophyletic origin, possibly from the Ranorthidae, and thus only one superfamily need be used, as in the Treatise on Invertebrate Paleontology (Wright *in* Williams *et al.* 1965). In addition to the genera described in more detail below, *Dicoelosia*, *Laticrura*, and *Epitomyonia* have all been found as relatively rare components of the fauna at several localities. Although the enteletaceans form the most numerous group of brachiopods in the late Ashgill of the Oslo-Asker area, they are also the most difficult to identify, partly because homoeomorphy is rife in some characters, partly because of the large number of generic and specific names available (perhaps indicating finer taxonomic splitting than in other brachiopod groups), and partly because different systematists have adopted different criteria in older and younger rocks, whilst leaving the Ashgill enteletaceans relatively poorly known, except those from Bohemia.

EXPLANATION OF PLATE 78

Figs. 1–4. *Trematis norvegica* sp. nov., all from 25 m above the base of the Langoyene Sandstone Formation, north shore of Hovedoya, Oslo, Grid Ref. NM 968416. 1, PMO 104.018, holotype, a pedicle valve, ×2. 2, BB 91667, a pedicle valve, ×2. 3, BB 76072, interior of a pedicle valve, ×4, showing ornament. 4, BB 76073, a brachial valve, ×1·5. Note that the specimens in figs. 2 and 4 have cornulitids attached to the interior of the valves.

Fig. 5. *Orthambonites* sp., BB 75311, the internal mould of a brachial valve, from Husbergøya Shales, 10 m above base of section at Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853403, ×4.

Figs. 6–10. *Hirnantia sagittifera* (M'Coy, 1851), from within 2 m of the base of the Langøyene Sandstone Formation, fig. 6 from west Rambergoya, Oslo, Grid Ref. NM 962394, figs. 7–10 from north-west Gressholmen, Oslo, Grid Ref. NM 963400. 6, PMO 104.019, internal mould of a pedicle valve, ×1·5. 7, BB 74616, internal mould of a pedicle valve, ×1. 8–10, BB 74123, internal mould of a particularly large and convex brachial valve, ×1.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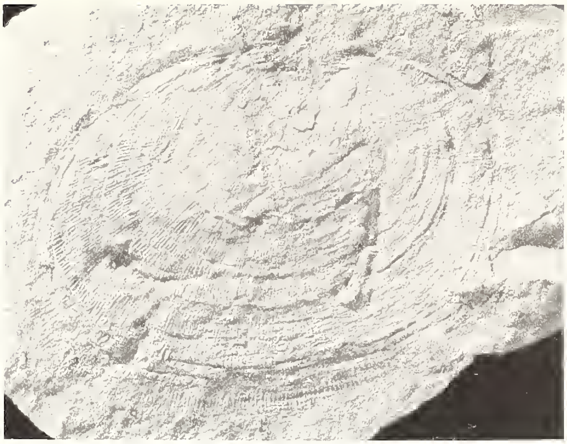
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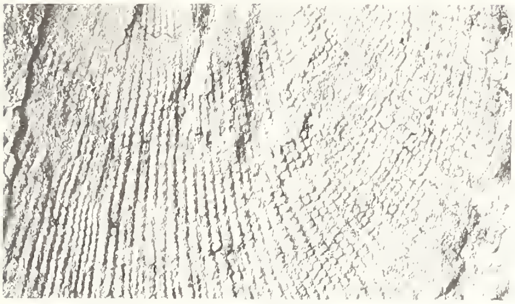
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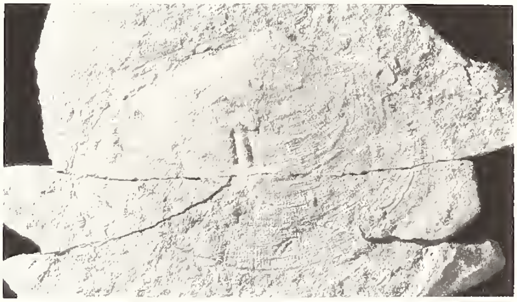
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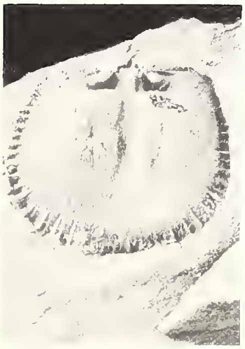
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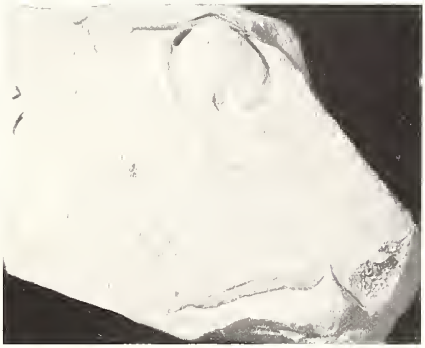
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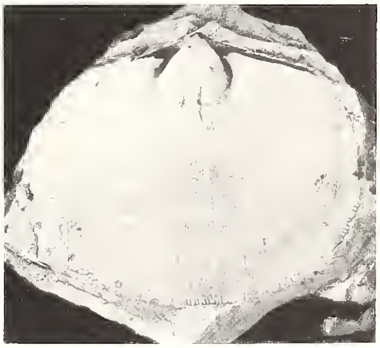
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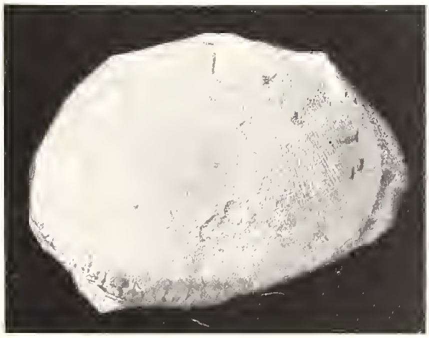
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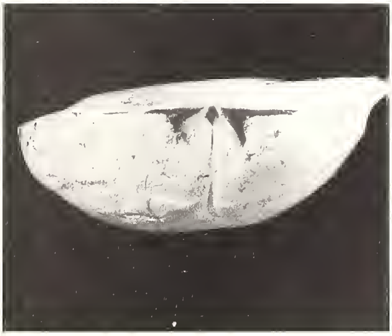
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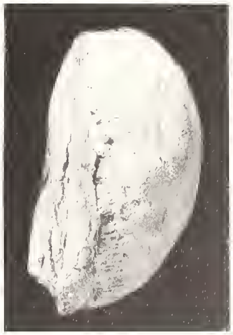
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COCKS, *Trematis*, *Orthambonites*, and *Hirnantia*

Family DALMANELLIDAE Schuchert, 1913
Genus DALMANELLA Hall and Clarke, 1892
Dalmanella testudinaria (Dalman, 1828)

Plate 79, figs. 4–12

1828 *Orthis testudinaria* Dalman, p. 115, pl. 2, figs. 4*a–e*.
1963 *Dalmanella testudinaria* (Dalman); Williams and Wright, p. 29, pl. 2, figs. 7, 8, 11–13, 16–19.
1965 *Dalmanella testudinaria* (Dalman); Temple, p. 383, pl. 3, figs. 1–7; pl. 4, figs. 1–6; pl. 5, figs. 1–7; pl. 6, figs. 1–7.
1968 *Dalmanella testudinaria* (Dalman); Bergström, p. 8, pl. 2, fig. 5.
1977 *Dalmanella testudinaria* (Dalman); Havlíček, p. 137, pl. 32, figs. 1–15, 18, 19, 23; pl. 56, fig. 13.
1980 *Dalmanella testudinaria* (Dalman); Nikitin *in* Appollonov *et al.*, p. 38, pl. 12, figs. 1–17.

Material. In the Oslo–Asker district, *D. testudinaria* is common at a number of localities, particularly at 1–5 m above the base of the Langøyene Sandstone, e.g. at Gressholmen (BB 74131–74160), Grid Ref. NM 962399, Husbergøya (BB 74231–74247), Grid Ref. NM 961376, and Hoyerholmen (BB 75572–75602, BB 75960–75968), Grid Ref. NM 874361.

Discussion. Since the species has been extensively redescribed in recent years (see selected synonymy above), a full description is not given here. *Dalmanella* was a variable and successful genus from Llanvirn to early Llandovery times, and its great variability, as well as its sheer abundance from many localities, has presented problems to many taxonomists. In late Ashgill times, *D. testudinaria* was particularly widespread, and is known both as an important constituent of the *Hirnantia* community, and as a significant, sometimes even dominant, member of other assemblages. It has been found in a wide variety of lithologies, ranging from siltstones (e.g. Västergötland, Poland, Bohemia, Aber Hirnant) to fine calcilutites (the type locality at Borenshult, Sweden, and the Oslo–Asker district) and micrites (Anticosti Island, Canada). Mitchell (1977) distinguished a subspecies for slightly wider forms, later renamed (Mitchell *in* Cocks 1978, p. 63) *D. testudinaria ripae*, from the Pomeroy area, Ireland, and Dr. D. A. T. Harper tells me that this is also the common form in the Whitehouse Group of Girvan, Scotland. Other closely related contemporary forms include *D. edgewoodensis* Savage, from central North America and reviewed by Amsden (1974), whose brachial valve is more convex and less sulcate than *D. testudinaria*; *D. portranensis*,

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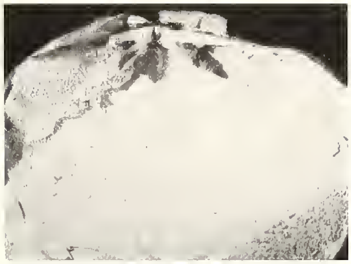
EXPLANATION OF PLATE 79

Figs. 1–3. *Hirnantia sagittifera* (M'Coy, 1851), from within 2 m of the base of the Langøyene Sandstone Formation, figs. 1 and 2 from north-west Gressholmen, Oslo, Grid Ref. NM 963400, fig. 3 from west Rambergøya, Oslo, Grid Ref. NM 962394. 1, BB 74116, latex cast of the internal mould of a brachial valve, with encrusting ceramoporoid bryozoan, × 1·5. 2, BB 93984, latex cast of the external mould of a brachial valve, × 1·5. 3, BB 74115, latex cast of the internal mould of a brachial valve, × 1·5.

Figs. 4–12. *Dalmanella testudinaria* (Dalman, 1828), all from within 2 m of the base of the Langøyene Sandstone Formation, north-west Gressholmen, Oslo, Grid Ref. NM 963400. 4, BB 74148, internal mould of a pedicle valve, × 3. 5, BB 74136, latex cast of the external mould of a brachial valve and associated pedicle valve interarea, × 3. 6, 7, BB 74145, internal mould of a pedicle valve and the latex of it, × 2·5. 8, BB 74144, internal mould of a brachial valve, × 3. 9, 10, BB 74152, latex cast and internal mould of a brachial valve, × 3. 11, 12, BB 74151, latex cast and internal mould of a brachial valve, × 3.

Figs. 13, 14, 17, 18. *Onniella kalvoya* sp. nov., all from Langøyene Sandstone Formation, 24 m above the base of Stage 5, Kalvoya north-east, Baerum, Grid Ref. NM 864401. 13, 14, PMO 104.021, holotype, internal mould of a brachial valve and latex cast of the corresponding external mould, × 3. 17, BB 91890, internal mould of a brachial valve, × 3. 18, BB 91885, internal mould of a pedicle valve, × 3.

Figs. 15, 16. *Drabovia* sp., from Husbergøya Shale Formation, 1 m below brown sandstone at the top of the formation, south-west coast of Bronnøya, Asker, Grid Ref. NM 857362. 15, BB 74649, internal mould of a brachial valve, × 3. 16, BB 74647, internal mould of a pedicle valve, × 3.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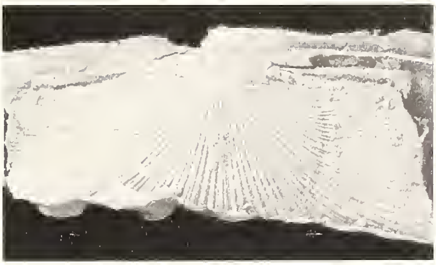
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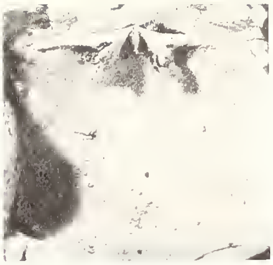
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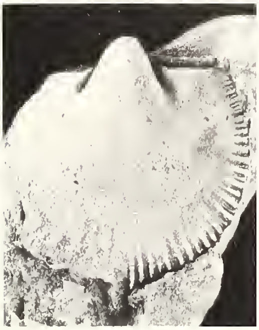
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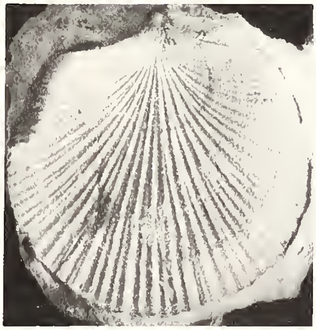
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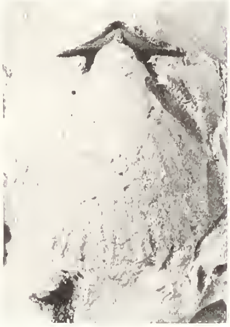
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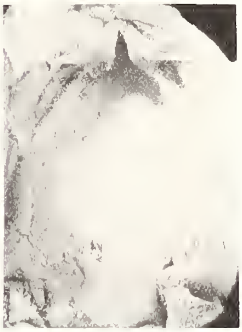
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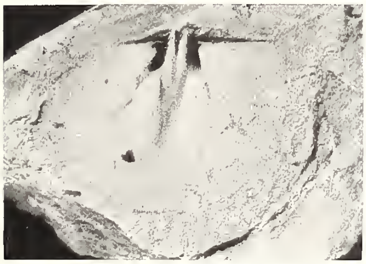
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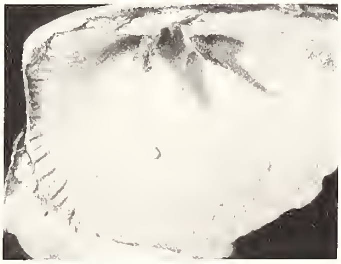
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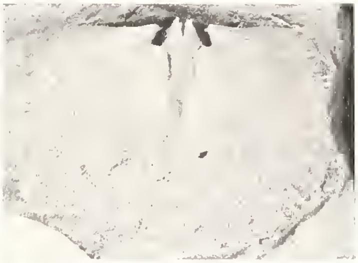
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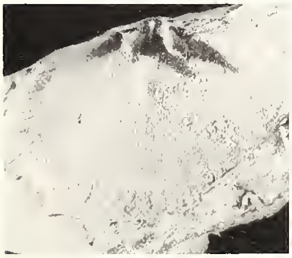
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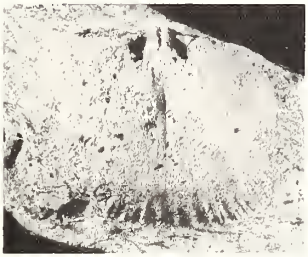
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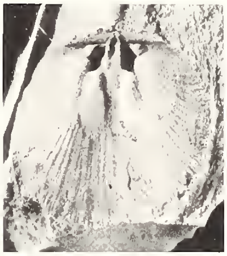
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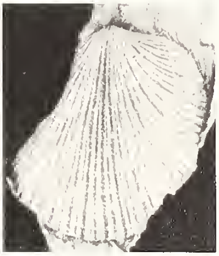
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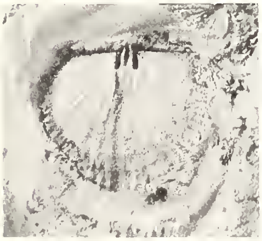
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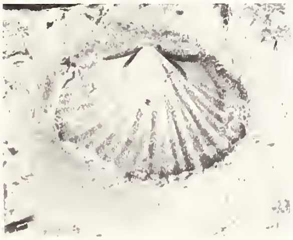
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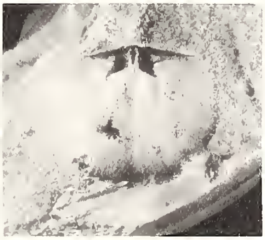
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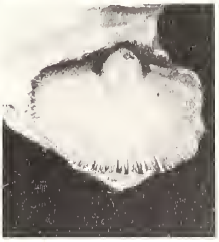
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COCKS, *Hirnantia*, *Dalmanella*, *Onniella* and *Drabovia* whose dental lamellae are more nearly parallel and whose brachiophores are longer than *testudinaria* (Wright 1964); and *D. wysogorskii*, from Swedish erratic blocks of the same age as the Leptaena Limestone of Dalarna (Wiman 1907), which needs revision. *D. cicatrica*, from Kazakhstan (Nikitin *in* Appollonov, Bandaletov and Nikitin 1980), and *D. pectinoides* Bergström, 1968, from Västergötland, both differ in ribbing style, and *D. pectinoides* also in the form of the muscle field in the pedicle valve. *D. testudinaria* itself is a very variable form, and although several authors have presented statistical analyses of various sorts, it is instructive to note the variability in the relative sizes and proportions of the cardinal process, brachiophores, shaft and median ridge (compare Pl. 79, figs. 9 and 11 with Williams and Wright 1963, pl. 2, figs. 7 and 8).

Genus ONNIELLA Bancroft, 1928

Onniella kalvoya sp. nov.

Plate 79, figs. 13, 14, 17, 18; Plate 80, figs. 1–5

Description. Exterior. Shells with subcircular outline; gently convex pedicle valve without incurved umbo; convex brachial valve with gentle sulcus. Relatively small apsacline pedicle valve interarea, narrow open delthyrium, with apex angle about 40°. Small anacline brachial valve interarea, approximately half valve width; open notothyrium partly filled with posterior of cardinalia. Primary ornament of relatively fine, even costellae (approx. 5 per mm at 3 mm anteriorly) with new ribs arising by branching; secondary ornament of concentric filae (14–16 per mm throughout valve length) more accentuated in rib troughs and rarely crossing rib crests.

Pedicle valve interior. Strong teeth supported by short stubby dental plates which merge anteriorly quickly with the valve floor; small crural fossettes present. Muscle field relatively small, extending for average of 34% valve length in five specimens, bilobed, adductor scars poorly differentiated (Pl. 79, fig. 17). Vascular markings usually obscure, but pair of thick *vascula media* diverge anteriorly from diductor scars in some specimens.

Brachial valve interior. Cardinal process relatively small, bilobed posteriorly, and continuing anteriorly in a thin shaft which merges further anteriorly with a low but distinct myophragm. Thick, stubby brachiophores which merge posterolaterally with subsidiary fulcral plates to give well-defined sockets, which are also bounded anterolaterally by thin socket plates. Tops of brachiophores diverging anteriorly at about 70°. Well-defined adductor area extending anteriorly for 50–60% of valve length; anterior scars longer and wider than posterior scars (Pl. 79, fig. 13).

Material. Holotype PMO 104.021, the internal mould and external counterpart of a brachial valve (Pl. 79, figs. 13, 14): 9 conjoined valves, 13 pedicle valves, and 7 brachial valves (including BB 74248–74253, BB 91874–91892) from the Langåra Limestone-Shale Formation, 24–26 m above the base of Stage 5, north-east end of Kalvoya, Baerum, Norway, Grid Ref. NM 864401. The species also occurs commonly at other localities in the same formation, and rarely in the Husbergøya Shales.

Dimensions (in mm)	Length	Width
PMO 104.021, brachial valve, holotype	9.9	9.5
BB 91890, brachial valve	6.3	7.1
BB 74253, brachial valve	9.5	11.6
BB 91885, pedicle valve	7.3	8.4
BB 91881, pedicle valve	12.6	*c.* 12

Discussion. Seven species of *Onniella* are known from the Caradoc of Britain (Cocks 1978; Hurst 1979), four from North America (Cooper 1956), five from Bohemia (Havlíček 1977), and seven from the Baltic area (Hints 1975). However, since '*Onniella*' *rava* and its subspecies *silvicola*, known from Ashgill and early Llandovery rocks in Bohemia and Wales (Marek and Havlíček 1967; Temple 1970), have been transferred to *Ravozetina* by Havlíček (1977, p. 145), the only nominal post-Caradoc species are the five revised by Hall (1962) from the Cincinnatian of eastern North America and *O. trigona* and *O. mediocra* from the Llandovery of Estonia (Rubel 1962); the former also identified in the late Ashgill of Estonia and Latvia by Hints (1975). This substantial and important stock needs revision as a whole; nevertheless, *O. kalvoya* appears to be different from other species in its combination of relatively finely spaced primary ribbing with the fine secondary concentric filae. The filae have also been reported in Ashgill *O. trigona* by Hints (1975, pl. 11, fig. 8*a*), but that species has coarser primary ribs, stronger brachiophores, and a larger myophragm than *O. kalvoya*.

Genus PAUCICRURA Cooper, 1956
Paucicrura sp.

Plate 80, figs. 6, 7

Discussion. Shells like BB 73781–73792, from near the top of the Langoyene Sandstone, 72–73 m above the base of Stage 5, to the south-west of Rambergoya, Oslo, Grid Ref. NM 962394, can be firmly attributed to *Paucicrura*, possessing as they do a trilobed cardinal process and flaring brachiophores like the type species *P. rogata* (Sardeson, 1892) from the Trenton of Minnesota (Cooper 1956, pl. 157F, figs. 18–24). The distinctive brachial valve sulcus is also present in the Norwegian specimens. Lack of recent revision of the genus precludes specific attribution at present; however, the Norwegian specimens appear to be the stratigraphically youngest so far attributed to *Paucicrura*, whose upper limit was previously uncertain (Cooper 1956, p. 143). The species is known from various localities and horizons within the Oslo-Asker area, for example half-way up Stage 5 at the Høvikveien–Baerumsveien road junction, Baerum, Grid Ref. NM 885431.

Family DRABOVIIDAE Havlíček, 1951
Genus DRABOVIA Havlíček, 1951
Drabovia sp.

Plate 79, figs. 15, 16

Discussion. Relatively rare shells, like BB 74647–74649 from 1 m below the brown sandstone at the top of the Husbergoya Shales at a roadside exposure in south-west Bronnoya, Asker, Grid Ref. NM 858363, can be assigned to the Draboviidae, and seem best attributed to *Drabovia* itself on the basis of their cardinalia, brachiophore shape, and ornament. This genus ranges from the Llandeilo to the Ashgill (Havlíček 1977, p. 244), and the brachial valve illustrated here (Pl. 79, fig. 15) is very comparable to *D. westrogothica*, which was described by Bergström (1968) from the late Ashgill of Västergötland, Sweden.

Genus HIRNANTIA Lamont, 1935
Hirnantia sagittifera (M'Coy, 1851)

Plate 78, figs. 6–10; Plate 79, figs. 1–3; Plate 80, fig. 8

1851 *Orthis sagittifera* M'Coy, p. 398.
1935 *Hirnantia sagittifera* (M'Coy); Lamont, p. 313, pl. 7, figs. 20–22.

Description. Exterior. Biconvex, with convexity of brachial valve considerably greater than pedicle valve. Faint trace of very weak pedicle valve fold and corresponding brachial valve sulcus seen in a few valves only. Small anacline brachial valve interarea and fairly small apsacline pedicle interarea. Open delthyrium with small pedicle collar and open notothyrium. Relatively fine radial ornament (84 ribs counted at 10 mm growth line on BB 93984, Pl. 79, fig. 2), with new costellae arising both by bifurcation and intercalation, the costellae curving round laterally to merge with the hinge line. Growth lines obscure, except anteriorly in old specimens.

Pedicle valve interior. Teeth supported by dental plates extending to the valve floor and diverging at right angles, merging antero-laterally with the variably developed muscle-bounding ridges. Thin lanceolate adductor muscle scars between well-impressed anteriorly rounded diductor muscle scars, the whole muscle field bilobed, and extending anteriorly for about one-third of the valve length. Vascular markings obscure.

Brachial valve interior. Cardinal process small, simple (Pl. 79, figs. 1, 3), becoming stronger and more bulbous in the most gerontic specimens (Pl. 78, fig. 9). Pair of stout but relatively short socket plates (the 'supporting plates' of Temple 1965, p. 400) diverging at right angles and attached to the valve floor. Variably developed, poorly defined, thin and low median septum extends for up to one-third of the valve length. Adductor muscle field weakly impressed, but each muscle scar is subcircular and extends anteriorly from between one-quarter and one-third of the valve length.

Material. PMO 104.019 (Pl. 78, fig. 6) and BB 75477–75485, BB 93947–93966 from Langoyene Sandstone Formation (basal Hirnantian), 1–2 m above brown sandstone, shore exposure at Rambergoya west, Oslo, Grid Ref. NM 962394. The species occurs at several localities at a similar horizon (see Brenchley and Cocks 1982), and particularly abundantly in an old quarry at Gressholmen (BB 74109–74130) at Grid Ref. NM 963400.

Dimensions (in mm)	Length	Width
PMO 104.019, internal mould of pedicle valve	28·2	*c.* 37
BB 74616, internal mould of pedicle valve	33·7	41·1
BB 74109, internal mould of pedicle valve	24·9	31·0
BB 74123, internal mould of brachial valve	33·3	45·6
BB 93964, internal mould of brachial valve	21·7	26·5

Discussion. Hirnantia sagittifera dominates the macroecology of the beds in which it occurs, both as a large species in its own right and also as the base for a common epifauna of ceramoporoid bryozoans, crinoids, cornulitids, and other forms which thrived on both live and dead *Hirnantia* shells. A fuller synonymy for the species is given in Cocks (1978, p. 79); it is well known from many studies, the topographically closest being that of Bergström (1968) from Västergötland, Sweden.

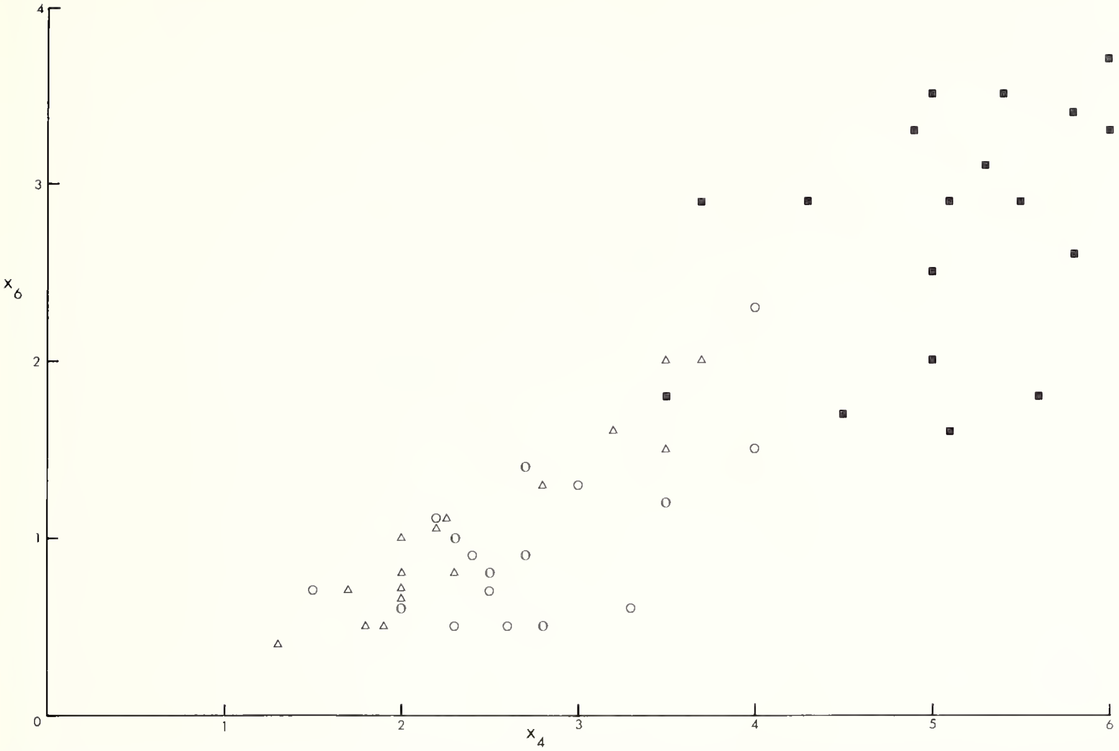
The Oslo shells are particularly large by comparison with other populations of *Hirnantia*, and thus statistical tests were made using the brachial valve parameters originally measured by Temple (1965, p. 400), i.e. x_4, the socket plate length; x_5, the socket plate width; and x_6, the crural pit depth, all measured from internal moulds (text-fig. 1). Dr. Temple has kindly provided me with his raw data from Hirnant, Wales (the type locality for *H. sagittifera*); Hol Beck, the English Lake District; and Stawy, Poland, to compare with the new data from the Oslo region (Table 1), and their allometry has been tested. When x_4 is compared with x_5, the Oslo slope is significantly different from the other three, but when x_4 is compared with x_6, then the Oslo shells are seen to group with the Welsh shells as against the Polish and Lake District specimens. The pooled slope of x_4 against x_6 is 1·75, and when the group means are adjusted using this slope then the Oslo and Welsh groups give intercepts on the vertical through $\log x_4 = 0$ of $-1{\cdot}86$ and $-1{\cdot}83$, which are statistically significantly different from the Polish and Lakes groups, which both give valves of $-1{\cdot}51$. Some thought was given to the possibility of erecting a new subspecies for the larger and also proportionately different Oslo material, but this was rejected in favour of recognizing *H. sagittifera* as a rather variable species tolerating a relatively wide range of habitats and temperature conditions, of which the warm lime muds of the Oslo area apparently represented the optimum. Rong (1979) erected a new species *H. magna* and another new subspecies *H. sagittifera fecunda* based on Chinese material of similar age, but his illustrations suggest that both forms and their names can be included within *H. sagittifera sensu stricto* as interpreted herein.

Family LINOPORELLIDAE Schuchert and Cooper, 1931
Genus LEPTOSKELIDION Amsden, 1974
Leptoskelidion loci sp. nov.

Plate 80, figs. 9–14

Description. Exterior. Biconvex shells with subcircular but slightly transverse outline and short hinge line; no trace of fold or sulcus. Small anacline brachial valve interarea and fairly small curved apsacline pedicle valve interarea. Open delthyrium and notothyrium. Weak ribs, 6 per mm at 3 mm anteriorly from the umbo; ribs curving round laterally but not merging with hinge line. Growth lines obscure.

Pedicle valve interior. Teeth large, supported by prominent but slender dental plates initially diverging at approx. 40° and curving anteriorly (sometimes changing direction at a single sharp point) to diverge for about 20° for most of their length (even slightly incurving in two specimens) before merging quickly anteriorly with



TEXT-FIG. 1. Relative dimensions of brachial valve structures of *Hirnantia sagittifera* from various localities: plot of x_4, the socket plate length, against x_6, the crural pit depth, for populations from Oslo (solid black squares), Hirnant, Wales (open circles), and Stawy, Poland (open triangles). The Polish and Welsh data and the definitions of x_4 and x_6 are from Temple (1965).

TABLE 1. Measurements of x_4, the socket plate length; x_5, the socket plate width; and x_6, the depth of the crural pit, of samples of *Hirnantia sagittifera* from Oslo, Wales, Poland, and the English Lake District. All on natural log scale. The intercepts are on the vertical lines corresponding to log $x_4 = 0$ in each case.

	Oslo	Wales	Poland	Lakes
Sample size (brachial valves)	18	17	20	17
x_4 (means and standard deviations)	1·61 (0·15)	0·98 (0·25)	0·67 (0·41)	1·08 (0·34)
x_5 (means and standard deviations)	−0·60 (0·45)	−1·02 (0·25)	−1·75 (0·49)	−1·09 (0·55)
x_6 (means and standard deviations)	0·97 (0·28)	−0·12 (0·44)	−0·33 (0·72)	0·38 (0·47)
Pairwise correlations x_4, x_5	0·55	0·87	0·76	0·82
Pairwise correlations x_4, x_6	0·36	0·53	0·96	0·93
Pairwise correlations x_5, x_6	−0·05	0·28	0·69	0·80
Allometric slope (from major axis) x_6/x_4	3·83	2·66	1·81	1·44
Intercept (plus or minus standard error)	−1·86 (0·07)	−1·83 (0·10)	−1·51 (0·05)	−1·51 (0·06)
Allometric slope (from major axis) x_5/x_4	5·00	2·07	1·28	1·78
Intercept (plus or minus standard error)	−4·11 (0·09)	−3·15 (0·06)	−3·21 (0·14)	−3·43 (0·10)

the valve floor. Muscle field less than one-third valve length, but details of musculature obscure. Vascular markings usually obscure, apart from traces of vascula media in a few specimens immediately anteriorly of the muscle field.

Brachial valve interior. Cardinal process thin and blade-like, merging anteriorly with the median septum which swells to a maximum thickness at about 3 mm anteriorly from the umbo and extends for up to half the valve length. The expanded brachiophore bases are subparallel posteriorly and then curve round to converge anteriorly and join the median septum in a well-defined sessile cruralium. The brachiophore bases also extend laterally to fuse with the hinge line to form prominent socket plates. Suboval adductor muscle scars poorly impressed on either side of the median septum anterior to the sessile cruralium.

Material. Holotype PMO 104.022, the internal mould of a brachial valve (Pl. 80, fig. 12) from a channel fill at the top of the Langøyene Sandstone Formation, 6 m below the local base of the Silurian at south-west Hovedoya, Oslo, Grid Ref. NM 966407, and thirty-seven other specimens from the same locality (including BB 70367–70378, BB 70402–70409, BB 75998–76004), and other channels nearby (e.g. BB 35300–35304). The species also occurs rarely in the top sandstone of the couplet at the very top of the same formation, for example at south-east Langøyene, Nesodden, Grid Ref. NM 968385 (e.g. BB 74280).

Dimensions (in mm)	Length	Width
PMO 104.022, internal mould of a brachial valve, holotype	11·3	14·8
BB 70403, internal mould of a brachial valve	14·5	16·4
BB 70367, external mould of a brachial valve	10·1	*c.* 15
BB 70370, internal mould of a pedicle valve	13·9	14·8
BB 76001, internal mould of a pedicle valve	15·8	*c.* 17

Discussion. Leptoskelidion loci is closely related to the type and only other known species of the genus, *L. septulosum* Amsden from the Noix Limestone of Missouri (Amsden 1974). However, the ornament of *L. loci*, although still weak, is stronger than on *septulosum*; the 'bulb-like myophore'

EXPLANATION OF PLATE 80

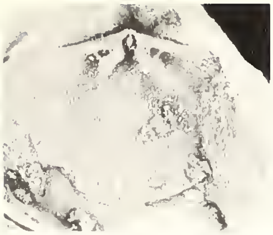
Figs. 1–5. *Onniella kalvoya* sp. nov., all from Langøyene Sandstone Formation, 24 m above the base of Stage 5, Kalvoya north-east, Baerum, Grid Ref. NM 864401. 1, BB 91890, latex cast of the internal mould of a brachial valve, × 4. 2, 3, BB 74253, internal mould and latex cast of a brachial valve, ×2. 4, BB 74250, latex cast of the exterior of a pair of conjoined valves, showing interarea (interarea broken to the right), ×3. 5, BB 91884, internal mould of a brachial valve, ×3.

Figs. 6, 7. *Paucicrura* sp., from Langoyene Sandstone Formation, 1 m below the top of the formation, south-west Rambergoya, Oslo, Grid Ref. NM 962393. 6, BB 73785, internal mould of a pedicle valve, ×3. 7, BB 73783, internal mould of a brachial valve, × 3.

Fig. 8. *Hirnantia sagittifera* (M'Coy, 1851), BB 74615, internal mould of a brachial valve, ×2, from within 2 m of the base of the Langoyene Sandstone Formation, north-west Gressholmen, Oslo, Grid Ref. NM 963400.

Figs. 9–14. *Leptoskelidion loci* sp. nov., all from channel fill 6 m below the top of the Langoyene Sandstone Formation, south-west Hovedøya, Oslo, Grid Ref. NM 966407. 9, BB 70370, internal mould of a pedicle valve, ×2. 10, 13, BB 70403, internal mould of a brachial valve and latex cast of the cardinalia, ×2·5. 11, BB 70369, latex cast of the external mould of a brachial valve, showing faint radial ornament, ×2. 12, PMO 104.022, holotype, internal mould of a brachial valve, ×2. 14, BB 70377, internal moulds of brachial valve (above) and pedicle valve (below), ×2.

Figs. 15–17. *Cliftonia* aff. *psittacina* (Wahlenberg, 1818), figs. 15 and 17 from 1 m above brown sandstone near the base of the Langåra Limestone–Shale Formation, west Langåra, Asker, Grid Ref. NM 856356, fig. 16 from top 15 cm of Husbergoya Shale Formation, west Rambergøya, Oslo, Grid Ref. NM 962394. 15, BB 75691, posterior view of a pair of conjoined valves, ×3. 16, BB 93909, internal mould of a brachial valve, ×2. 17, BB 74619, internal mould of a pair of conjoined valves, with part of the pedicle valve broken away and showing the long cardinal process of the brachial valve, ×2.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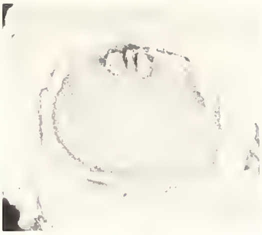
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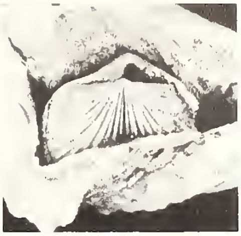
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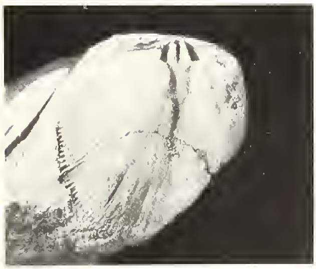
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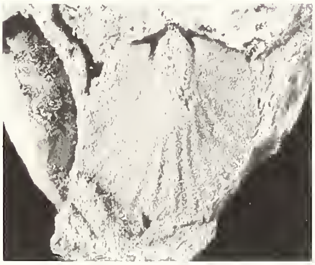
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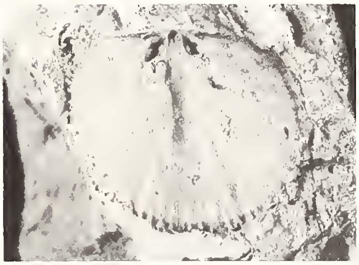
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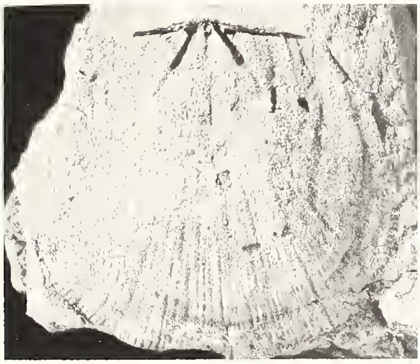
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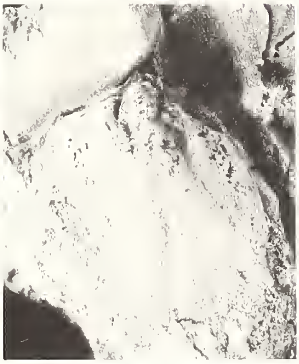
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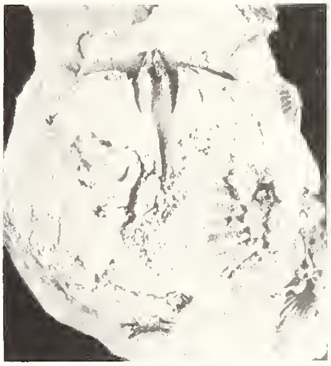
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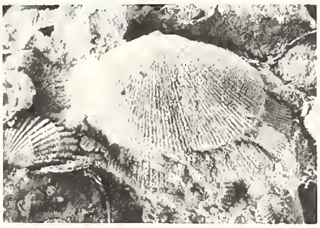
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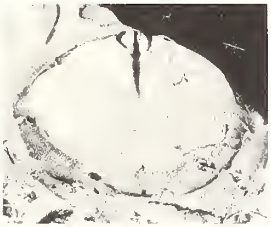
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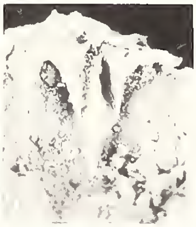
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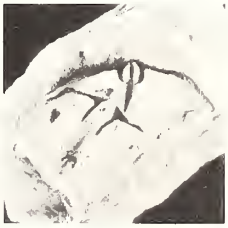
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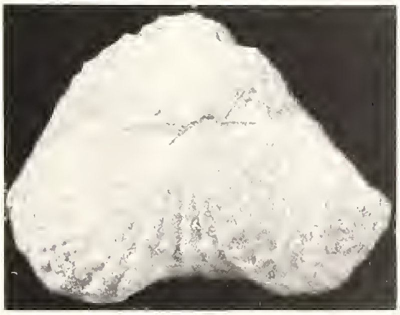
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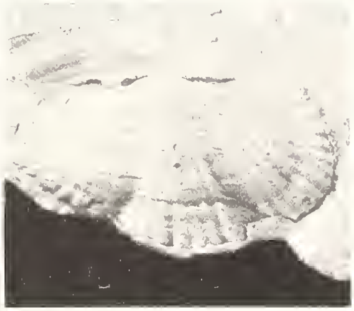
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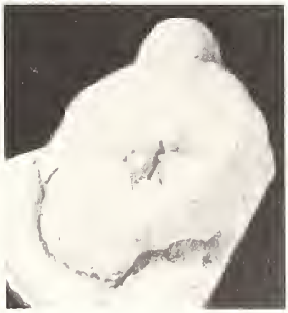
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COCKS, Enteletaceans and *Cliftonia*

of *septulosum* is much less pronounced than on *loci*; and the pedicle valve muscle-bounding ridge, which completely encircles the muscle field of *septulosum*, is scarcely developed in *loci*. The brachial valve median septum is also relatively shorter in *loci*. None of Amsden's specimens exceed 10 mm in width, whilst the Oslo material includes many shells nearly twice as large. *L. loci* is a minor constituent of the assemblage dominated by the rhynchonellide *Thebesia scopulosa*, and which appears to have lived in relatively shallow water.

Superfamily TRIPLECIACEA Schuchert, 1913
Family TRIPLECIIDAE Schuchert, 1913

Discussion. Apart from *Cliftonia*, discussed below and which occurs in swarms in some places, tripleciids occur rarely at most localities in the late Ashgill of the Oslo-Asker region. The most prevalent genus is *Triplesia* itself, tentatively identified here as *T.* aff. *insularis* (Eichwald, 1842) since some specimens appear externally similar to topotype *insularis* from Estonia: *Oxoplecia* is also known from several localities; and Wright (1965) has recorded the rare *Streptis undifera* (Schmidt, 1858) from 5*a* beds at Holmenskjaeret, Holmen, Asker.

Genus CLIFTONIA Foerste, 1909
Cliftonia aff. *psittacina* (Wahlenberg, 1818)

Plate 80, figs. 15-17

aff. 1818 *Anomites psittacinus* Wahlenberg, p. 65.
aff. 1968 *Cliftonia psittacina* (Wahlenberg); Bergström, p. 11, pl. 4, figs. 7-8; pl. 5, figs. 1, 2.

Discussion. At some localities in the middle of the Langåra Limestone-Shale Formation and in the Langøyene Sandstone Formation, *Cliftonia* occurs very commonly, for example at 1 m above the brown sandstone at Langåra west (Grid Ref. NM 856356), where it constituted 64% of the sample ($n = 171$). This is certainly the same species which occurs in the fauna from contemporary rocks in Västergötland, Sweden, which Bergström (1968) identified as *C. psittacina*, and for which he gave a full synonymy. However, the lectotype of *psittacina* comes from the Boda Limestone of Dalarna, Sweden, and without revision of the Boda form it is uncertain whether that material is specifically identical to specimens from Västergötland and the Oslo-Asker district: hence the Oslo-Asker material is left in open nomenclature.

Order STROPHOMENIDA Öpik, 1934
Superfamily PLECTAMBONITACEA Jones, 1928
Family LEPTELLINIDAE Ulrich and Cooper, 1936

Discussion. Leptellinids can be quite common in the area, particularly *Leangella* (Pl. 81, fig. 1), most of which are here identified as *L.* aff. *cylindrica* (Reed, 1917), which was originally described from the Shalloch Formation (Pusgillian) of Girvan, Scotland. *Diambonia* (Pl. 81, fig. 2) and *Sampo* (Pl. 81, fig. 3) also occur in smaller numbers. The *Sampo* is identified as *S. ruralis* (Reed, 1917), originally described from the Rawtheyan of Girvan and which appears to be a senior synonym of the type species *S. hiiuensis* from contemporary rocks in Estonia (Öpik 1933).

Family SOWERBYELLIDAE Öpik, 1930

In addition to the species of *Eoplectodonta* described below, *Eochonetes* (Pl. 81, fig. 4), *Thaerodonta*, *Sericoidea*, and *Chonetoidea* all occur sporadically in the Oslo-Asker area.

Genus EOPLECTODONTA Kozlowski, 1929

Eoplectodonta rhombica (M'Coy, 1852)

Plate 81, figs. 5, 6

1852 *Leptaena serica* var *a rhombica* M'Coy *in* Sedgwick and M'Coy, p. 239.
1871 *Leptaena sericea* var. *rhombica* M'Coy; Davidson, p. 325 *pars*, pl. 48, figs. 20–22, *non* figs. 10–19.
1928 *Sowerbyella rhombica* (M'Coy); Jones, p. 426, pl. 22, fig. 1.
cf. 1963 *Eoplectodonta* cf. *rhombica* (M'Coy); Williams, p. 448, pl. 12, figs. 9–14, 18, 19.
cf. 1977 *Eoplectodonta* (*Eoplectodonta*) cf. *rhombica* (M'Coy); Mitchell, p. 89, pl. 18, figs. 1–7.

Discussion. The lectotype of *rhombica* (selected by Jones 1928, p. 427) comes from the early Ashgill Crag Hill Beds of Horton-in-Ribblesdale, Cumbria. It is amongst the largest species in the whole family, often attaining widths of over 35 mm (e.g. BB 74577). In the Oslo–Asker area it is an intimate associate of *Holorhynchus* in the *Holorhynchus* beds near the top of the Langåra Limestone–Shale Formation, for example BB 74563–74577, BB 74594–74609 from the Ringeriksveien and Jongsåsveien, Sandvika, Baerum (Grid Ref. NM 852403 and NM 850400 respectively).

Eoplectodonta oscitanda sp. nov.

Plate 81, figs. 7–9

Description. Exterior. Concavo-convex shells of transverse outline: maximum width at hinge line. Pedicle valve interarea small, gently curved, apsacline: open delthyrium mostly filled by opposing chilidium of brachial valve. Brachial valve interarea small, catacline. Ornament of fine parvicostellae with density of 18–20 per 2 mm at 5 mm antero-medianly from umbo, and coarser costellae with 6–9 parvicostellae between each; new coarser costellae arising at intervals anteriorly to maintain a comparable distance between them throughout the valve length. Occasional traces of rugae developed in some specimens laterally. Growth lines obscure, except anteriorly in mature specimens.

Pedicle valve interior. Hinge line denticulate for one-third to one-half valve width, with 5–8 denticles seen on either side of the umbo. Teeth present, in one specimen (BB 75397) flaring anteriorly to form incipient muscle-bounding ridge, but this ridge is absent from the other shells. Flaring bilobed muscle field, deeply impressed and flabellate anteriorly (Pl. 81, fig. 7). Thick vascula media extend from anterior edge of muscle field. Median septum absent, apart from swelling between muscle scars at the very posterior of the valve.

Brachial valve interior. Hinge line fossettes corresponding with pedicle valve denticles. Trifid cardinal process with very slender central column, and the two lateral components strengthening and flaring antero-laterally to merge with the clavicular plates, whose posterior margins form the sockets. Edges of bema indistinct posteriorly, becoming stronger laterally and fading anteriorly. Inner side septa and outer side septa (Cocks 1970, p. 144) of variable strength, sometimes equal in size and at other times with the inner side septa considerably more prominent. Barely a trace of median septum developed in the centre of the valve in some specimens; apparently absent in others. Vascular system indistinct.

Material. Holotype PMO 104.023, the internal mould of a brachial valve (Pl. 81, fig. 8), and ten other brachial valves, four pedicle valves, and one pair of conjoined valves (including BB 71220–71229, BB 75395–75400), from the Langåra Limestone–Shale Formation, 18 m stratigraphically below the base of the *Holorhynchus* Beds, Ringeriksveien, Sandvika, Baerum (Grid Ref. NM 852403). The species also occurs sporadically at other localities in the same formation and in the Husbergoya Shale and Langoyene Formations.

Dimensions (in mm)	Length	Width
PMO 104.023, internal mould of brachial valve, holotype	7·0	15·1
BB 71228, external mould of a brachial valve	7·5	*c*. 15
BB 71220, external mould of conjoined valves	8·3	14·4
BB 75300, internal mould of a pedicle valve	8·6	13·4
BB 75301, internal mould of pedicle valve	8·7	15·2

Discussion. Relatively few species of *Eoplectodonta* have so far been described from rocks of Ashgill age. *E. oscitanda* differs from the widespread *E. rhombica* in its relatively more numerous major costellae, its more numerous and relatively finer secondary costellae, and in its smaller size. The new species may be conspecific with the *Eoplectodonta* sp. recently described by Hiller (1980, p. 183) from the Ashgill rocks of Glyn Ceiriog, Wales, although the parvicostella density appears greater in the Norwegian specimens. *E. clarksvillensis* (Foerste), from North America, requires revision, but it has common comae and the specimens seen are less incurved than *oscitanda*.

Superfamily STROPHOMENACEA King, 1846
Family STROPHOMENIDAE King, 1846

Discussion. Rare strophomenids occur throughout the area, but only *Leptaena* sp. is common enough to warrant description here. Genera identified include *Oepikina*, *Furcitella*?, *Katastrophomena*, *Kjerulfina*, *Kiaeromena*, and *Strophomena*. The specimens illustrated by Holtedahl (1916, pl. 8, figs. 7, 8) from 'Stage 5*a*, Nyborg and Bakke, Asker' as *S. asmusi* de Verneuil, 1845, appear attributable to *Strophomena sensu stricto*, although *asmusi* itself requires revision.

Leptaena sp.

Plate 81, figs. 13–15

Discussion. Leptaena occurs at many localities in the late Ordovician of the Oslo–Asker area, but unfortunately never in enough numbers at any one place to be able to characterize a new species. *Leptaena* sp. differs from the contemporary *L. rugosa* Dalman, 1828 of Västergötland, Sweden, revised by Bergström (1968), in its less regular rugae, and in the more elongate, as opposed to subcircular, pedicle valve muscle field. The only specimens similar to *L. rugosa* which are known from the area are some large specimens (e.g. BB 74589, over 50 mm wide) which were found in the base of the *Holorhynchus* Beds at the top of the Langåra Limestone–Shale Formation, and these are identified here as *L.* aff. *rugosa*.

EXPLANATION OF PLATE 81

Fig. 1. *Leangella* aff. *cylindrica* (Reed, 1917), BB 74349, internal mould of a pedicle valve, ×4, from 3 m above the base of the Langøyene Sandstone Formation, west Husbergøya, Nesodden, Grid Ref. NM 961375.

Fig. 2. *Diambonia* sp., BB 75298, internal mould of a pedicle valve, ×4, from 2 m above the base of the Husbergoya Shale Formation, west Langåra, Asker, Grid Ref. NM 856356.

Fig. 3. *Sampo ruralis* (Reed, 1917), BB 74690, internal mould of a pedicle valve, ×3, from 3 m above the base of the Husbergøya Shale Formation, south-east Brønnoya, Asker, Grid Ref. NM 869365.

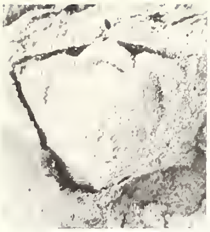
Fig. 4. *Eochonetes* sp., BB 91857, internal mould of a pedicle valve, showing the perforated hingeline, ×4, from 4 m above the base of the Husbergoya Shale Formation, north-east Kalvøya, Baerum, Grid Ref. NM 864401.

Figs. 5, 6. *Eoplectodonta rhombica* (M'Coy, 1852), from 3 m above the base of the *Holorhynchus* beds, Langåra Limestone–Shale Formation, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 5, BB 74567, latex cast of external mould of conjoined valves, ×2. 6, BB 73832, internal mould of a pedicle valve, ×2.

Figs. 7–9. *Eoplectodonta oscitanda* sp. nov., from the Langåra Limestone–Shale Formation, 18 m stratigraphically below the base of the *Holorhynchus* beds, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 7, BB 75301, internal mould of a pedicle valve, ×3. 8, PMO 104.023, holotype, the internal mould of a brachial valve, ×3. 9, BB 71220, latex cast of external mould of conjoined valves, ×2.

Figs. 10–12. *Christiania* sp., figs. 10 and 11 from 6 to 7 m above the base of the Langøyene Sandstone Formation, north shore of Hovedoya, Oslo, Grid Ref. NM 967416. 10, BB 76109, internal mould of a brachial valve, ×3. 11, BB 73777, internal mould of a pedicle valve, ×2. 12, BB 74703, internal mould of a pedicle valve, ×3, from 3 m above the base of the Husbergøya Shale Formation, north-east Kalvoya, Baerum, Grid Ref. NM 864401.

Figs. 13–15. *Leptaena* sp., from 3 m above the base of the *Holorhynchus* Beds, Langåra Limestone–Shale Formation, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 13, BB 94184, internal mould of a pedicle valve, ×2. 14, 15, BB 74556, external and internal moulds of a brachial valve, ×2.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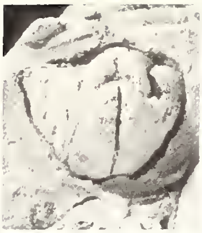
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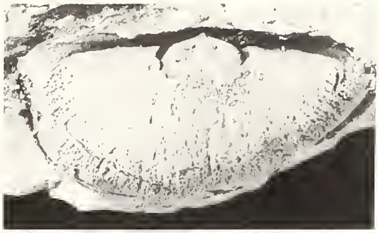
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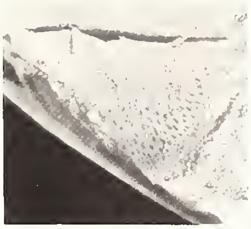
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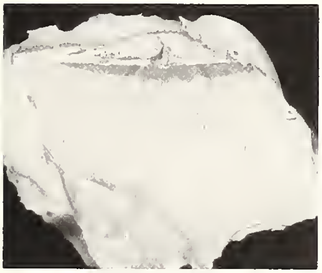
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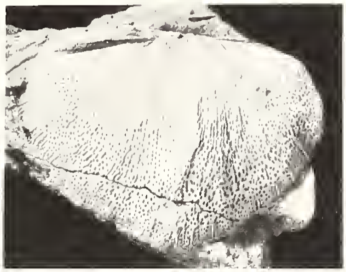
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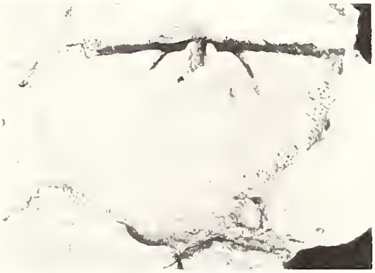
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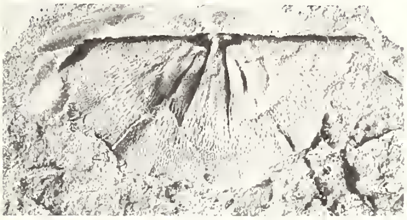
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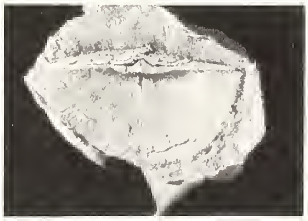
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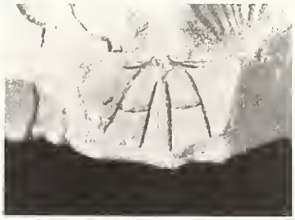
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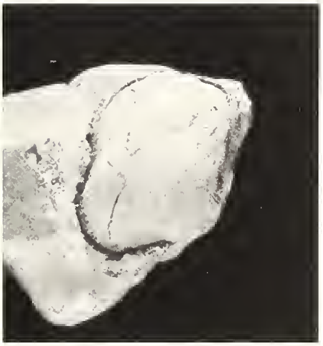
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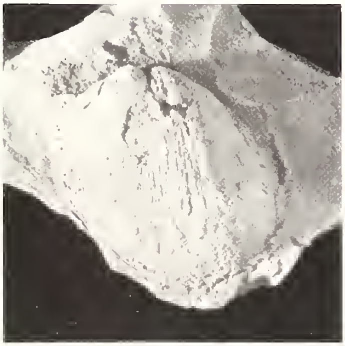
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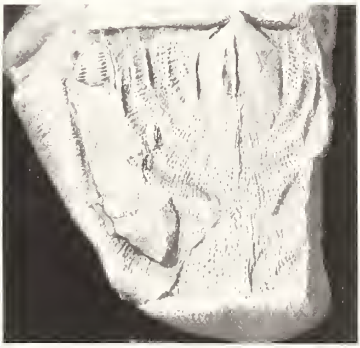
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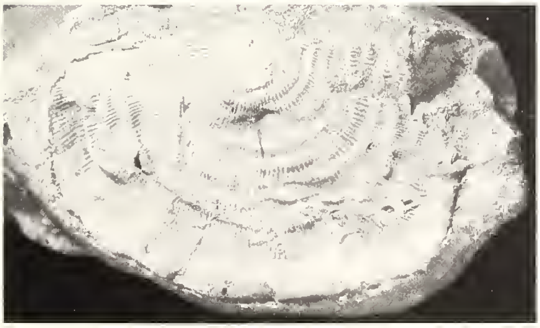
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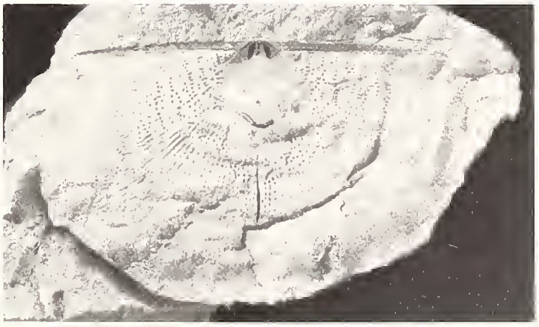
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COCKS, Strophomenides

Family CHRISTIANIIDAE Williams, 1953
Christiania sp.

Plate 81, figs. 10-12

Discussion. Identification of Ashgill *Christiania* is hampered by lack of revision of the much quoted but poorly known *C. tenuicincta* (M'Coy, 1844), originally described from the Kildare Limestone, Ireland. The chief distinguishing specific characteristic appears to be the presence and form of the subhorizontal septa in the brachial valve; other cited characters, such as the valve outline or the possession of a sulcus, appear to be less important. The genus is not common at most Oslo-Asker late Ordovician localities, but can be locally abundant, e.g. at 14·5 m above the base of the Langøyene Formation at Hovedøya north, Oslo (Grid Ref. NM 967416), where over fifty *Christiania* shells (including BB 76109-76116) were found concentrated into a single shell pocket. All these have variable subquadrate (Pl. 81, fig. 11) to semicircular (Pl. 81, fig. 12) outlines, and variably developed incipient sulci, and all the brachial valves had horizontal septa between the primary septa (Pl. 81, fig. 10), unlike the contemporary *C. portlocki* Mitchell, 1977.

Family STROPHEODONTIDAE Caster, 1939
Genus EOSTROPHEODONTA Bancroft, 1949
Eostropheodonta hirnantensis (M'Coy, 1851)

Plate 82, figs. 1-6

1851 *Orthis Hirnantensis* M'Coy, p. 395.
1871 *Strophomena siluriana* Davidson, p. 303, pl. 47, figs. 1-4.
1949 *Eostropheodonta whittingtoni* Bancroft, p. 9, pl. 2, fig. 6.

Discussion. A fuller synonymy may be found in Cocks (1978, p. 125), where Davidson's *siluriana* was provisionally regarded as a distinct subspecies, but close examination of topotype *hirnantensis*, *siluriana*, *whittingtoni*, and other samples from late Ashgill populations, including material from the Oslo-Asker district, has led to the conviction that only the one, rather variable, species of *Eostropheodonta* is present. In particular, the ribbing style, which characteristically consists of wavering costellae, is common to all of the samples. The species has also been illustrated from Västergötland, Sweden (Bergström 1968), Poland (Temple 1965), Czechoslovakia (Marek and Havlíček 1967), Wales (Cocks and Price 1975), and elsewhere, and is a common constituent of the *Hirnantia* Fauna. In the Oslo-Asker district it is relatively uncommon, and occurs chiefly as a

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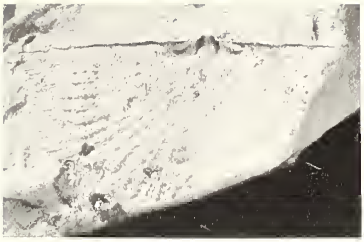
EXPLANATION OF PLATE 82

Figs. 1-6. *Eostropheodonta hirnantensis* (M'Coy, 1851), figs. 1-4 and 6 from coast section at west Rambergøya, Oslo, Grid Ref. NM 962394. 1-3, BB 94003, internal mould of a brachial valve and latex casts of its external and internal moulds, × 3, from 2 m above the base of the Langoyene Sandstone Formation. Figs. 4, 6, from 15 cms below the top of the Husbergøya Shale Formation. 4, BB 93972, latex cast of the external mould of a brachial valve. × 2. 6, BB 75492, enlargement to show internal mould of cardinalia, × 5. 5, BB 74289, internal mould of a pedicle valve, × 2, from 1 m above the base of the Langoyene Sandstone Formation, south-east coast of Langøyene, Nesodden, Grid Ref. NM 968385.

Figs. 7-13. *Coolinia dalmani* Bergström, 1968, all from 1 m below the top of the Husbergoya Shale Formation, south-west Bronnoya, Asker, Grid Ref. NM 859363. 7, BB 74636, internal mould of a pedicle valve, × 2. 8, BB 74626, latex cast of the external mould of a brachial valve, × 2. 9, BB 74632, internal mould of a pedicle valve, × 2. 10, BB 73776, latex cast of the external mould of a pedicle valve, × 2. 11, BB 74641, internal mould of a pedicle valve, × 2. 12, BB 74630, internal mould of a brachial valve, × 1·5. 13, BB 74629, internal mould of a brachial valve, × 2.

Figs. 14-16. *Brevilamnulella kjerulfi* (Kiaer, 1902), PMO 40466, syntype, conjoined valves, × 3, the original of Kiaer 1902 p. 64, figs. 5, 6, from Jorgenslökken, Asker.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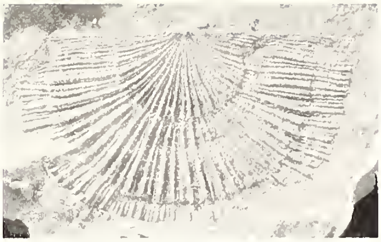
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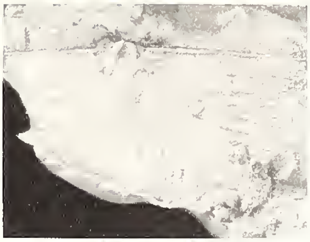
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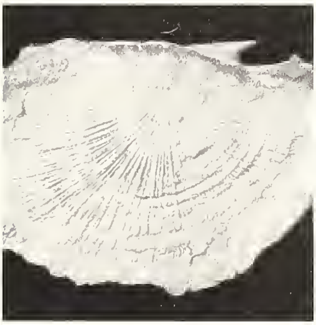
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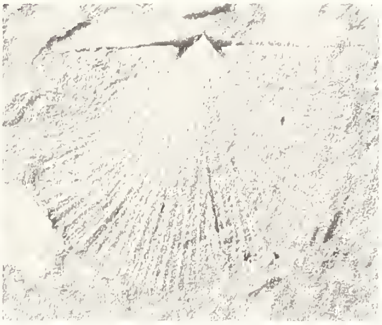
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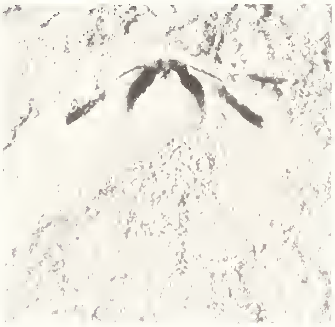
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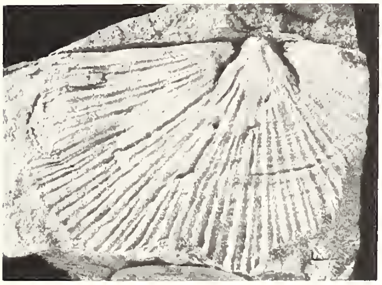
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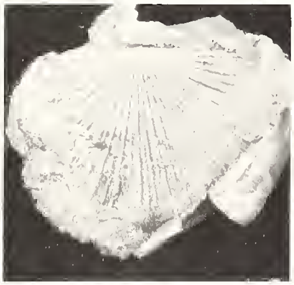
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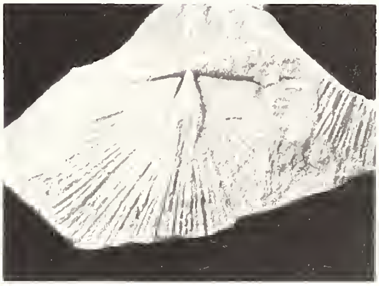
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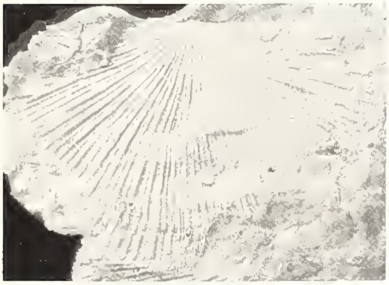
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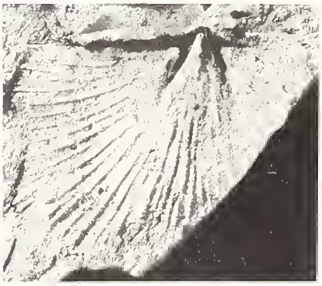
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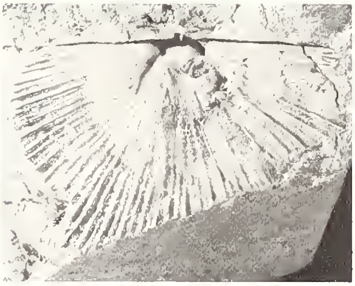
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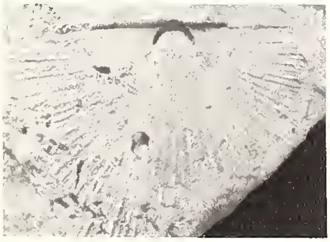
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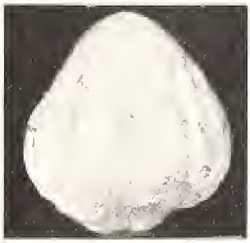
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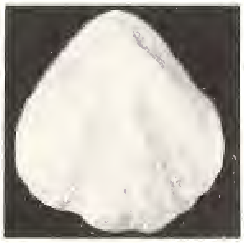
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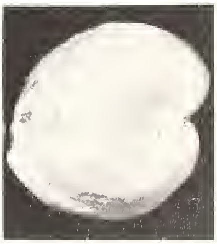
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COCKS, *Eostropheodonta*, *Coolinia* and *Brevilamnulella* minor constituent of the assemblages, but at some localities, e.g. near the base of the Langøyene Sandstone Formation at south-west Rambergøya, Oslo, Grid Ref. NM 962394, it can be abundant.

Superfamily DAVIDSONIACEA King, 1850
Family CHILIDIOPSIDAE Boucot, 1959
Genus COOLINIA Bancroft, 1949
Coolinia dalmani Bergström, 1968

Plate 82, figs. 7–13

1828	*Orthis? pecten* (Linnaeus) Dalman, pp. 110–111 *pars*, pl. 1, fig. 6*a–d*.
1968	*Coolinia dalmani* Bergström, p. 17, pl. 6, fig. 10; pl. 7, figs. 1–4.

Discussion. The chief difference between *Fardenia* and *Coolinia* lies in the chilidium, which is present in the latter and absent in the former. *C. dalmani* has a chilidium, but it is a very thin and fragile structure when compared with that of the Silurian *C. pecten*. The Oslo–Asker specimens may be confidently identified with Bergström's species not only in their brachial valve structures, valve form, and ribbing, but chiefly in the distinctive shape of their pedicle valve muscle-bounding ridges (Pl. 82, fig. 7), which distinguishes *C. dalmani* from all other species of the genus. In the Oslo–Asker District the species occurs sporadically, but is occasionally common, e.g. BB 74625–74642 from the top of the Husbergoya Shale Formation at south-west Brønnøya, Asker, Grid Ref. NM 858364.

Order PENTAMERIDA Schuchert and Cooper, 1931

Various pentamerides, in particular porambonitaceans such as *Parastrophina* and others (Wright 1974), occur very sporadically in the Oslo–Asker district, but the only abundant species are *Holorhynchus giganteus* and *Brevilamnulella kjerulfi*.

Superfamily PENTAMERACEA M'Coy, 1844
Family STRICKLANDINIIDAE Hall and Clarke, 1894
Genus HOLORHYNCHUS Kiaer, 1902
Holorhynchus giganteus Kiaer, 1902

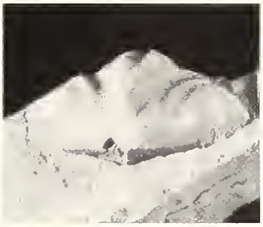
Plate 83, figs. 12–17

1902	*Holorhynchus giganteus* Kiaer, p. 68, figs. 1–7.
1938	*Holorhynchus giganteus* Kiaer; St. Joseph, p. 292, pl. 4, figs. 1–5.

EXPLANATION OF PLATE 83

Figs. 1–11. *Brevilamnulella kjerulfi* (Kiaer, 1902), figs. 1–4 and 8, from near the top of the Langåra Limestone–Shale Formation, roadside exposure south of Semsvatnet, Asker, Grid Ref. NM 799364, figs. 5–7, and 9–11 from south shore of Semsvatnet, Grid Ref. NM 800364, from about 20 m stratigraphically higher than the previous specimens. 1, 2, BB 93757, posterior and vertical views of the internal mould of a brachial valve, ×2. 3, BB 91591, internal mould of a pedicle valve, ×2. 4, 8, BB 91603, vertical and posterior views of conjoined valves, ×3. 5–7, BB 91574, three views of a partly exfoliated pair of conjoined valves, ×2. 9, BB 91576, internal mould of a brachial valve, ×2. 10, 11, BB 91585, vertical and posterior views of the internal mould of a brachial valve, ×2.

Figs. 12–17. *Holorhynchus giganteus* Kiaer, 1902. 12, PMO 73241, posterior view of a prepared pedicle valve, ×1, the original of Kiaer 1902, p. 73, fig. 5, from *Holorhynchus* beds, Sandviksåsen, Baerum. Figs. 13–15 from 3 m above the base of the *Holorhynchus* beds, Langåra Limestone–Shale Formation, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 13, BB 73774, internal mould of a pair of conjoined valves of a small, presumably young, individual, ×2. 14, BB 73775, internal mould of the posterior part of a brachial valve demonstrating its similarity to a stricklandiid, ×2. 15, BB 74526, posterior view of the internal mould of an adult pedicle valve, ×1. 16, 17, PMO 12431, lectotype, conjoined valves, the original of Kiaer 1902, pp. 70, 71, figs. 1–3, ×1, from *Holorhynchus* beds, Aspelund, Asker.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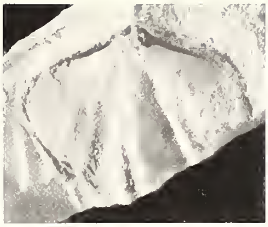
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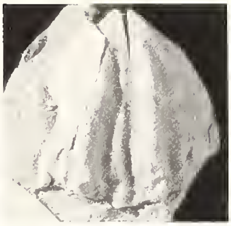
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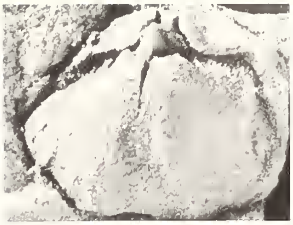
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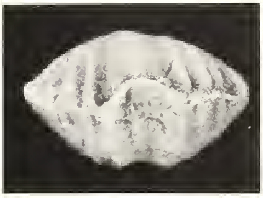
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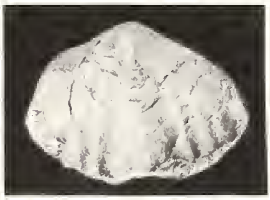
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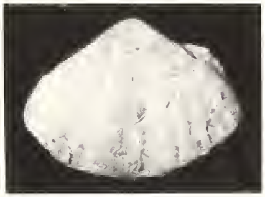
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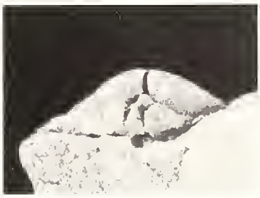
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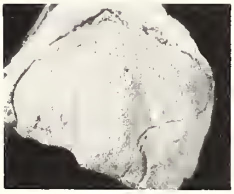
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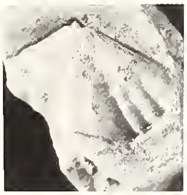
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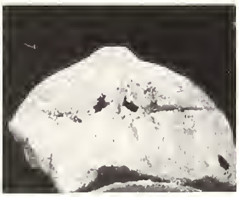
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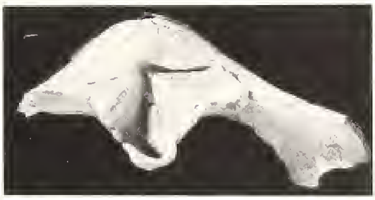
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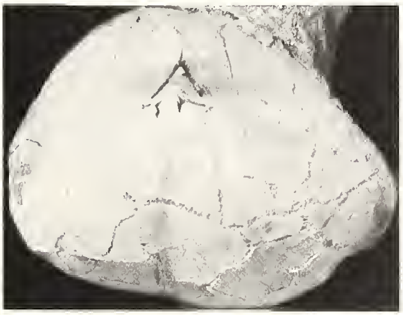
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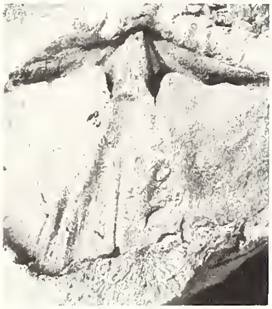
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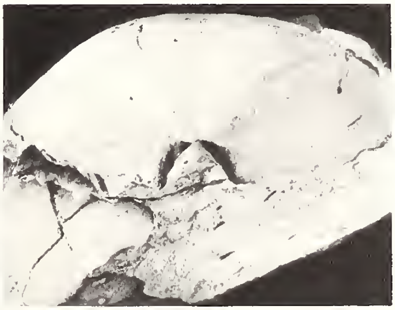
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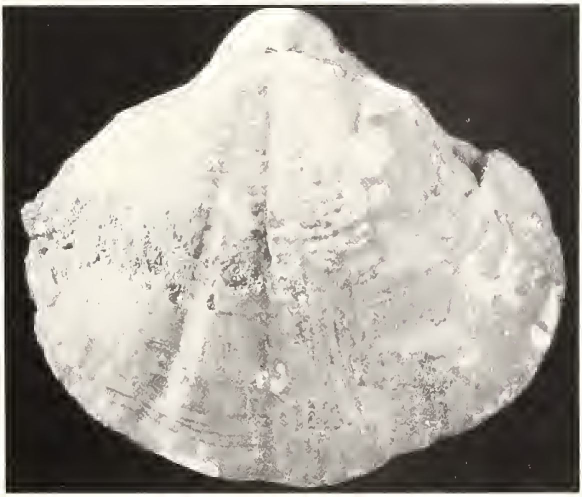
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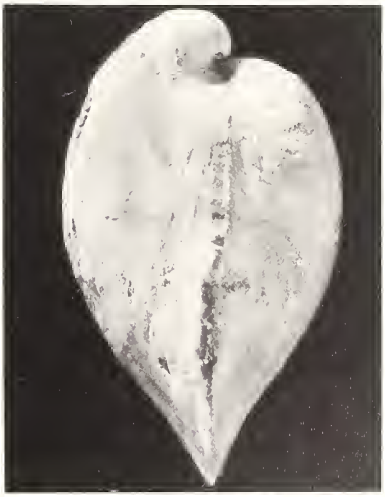
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COCKS, *Brevilammulella* and *Holorhynchus*

Remarks. The opportunity is taken here, not only of refiguring the lectotype, PMO 12431 (selected St. Joseph 1938, p. 293), which is a typical large specimen of conjoined valves with full calcite, but also of figuring the interior of the brachial valve for the first time (apart from serial sections), in both half-grown (Pl. 83, fig. 13) and fully mature (Pl. 83, fig. 14) specimens. It can be seen that the brachial valve interior of the mature specimen is virtually identical to brachial valves of the early Llandovery *Stricklandia lens lens* (J. de C. Sowerby, 1839), and indeed the pedicle valve structures are also similar, apart from the median septum, which is strong but short in *Stricklandia*, and virtually absent in mature *Holorhynchus* (Pl. 83, fig. 15), although weakly present in juveniles (Pl. 83, fig. 13) The similarities are close enough to transfer *Holorhynchus* unequivocally from the Pentameridae or the Virgianidae, where it had been classified by most authors, into the Stricklandiniidae, where its phylogenetic position needs reassessment among other late Ordovician genera such as *Prostricklandia* and others (Sapelnikov and Rukavishnikova 1975). In the Oslo-Asker district, millions of *Holorhynchus* shells dominate a widespread assemblage in the *Holorhynchus* Beds at the top of the Langåra Limestone-Shale Formation to the west of the area.

?Family VIRGIANIDAE Boucot and Amsden, 1963

Genus BREVILAMNULELLA Amsden, 1974

Brevilamnulella kjerulfi (Kiaer, 1902)

Plate 82, figs. 14-16; Plate 83, figs. 1-11

1902 *Barrandella kjerulfi* Kiaer, p. 63, figs. 1-7.
1938 *Clorinda kjerulfi* (Kiaer); St. Joseph, p. 307, pl. 7, figs. 1-6; pl. 8, figs. 1-13.

Discussion. At first sight, comparison is difficult between the reconstructions from the serial sections of *kjerulfi* given by St. Joseph (1938, pl. 7), and the interior views of silicified specimens given by Amsden (1974, pls. 1, 2) of the type, and hitherto only known, species of *Brevilamnulella*, *B. thebesensis* (Savage, 1913) from the late Ordovician Edgewood Formation of Missouri and Illinois and the Keel Formation of Oklahoma. However, there is no doubt that, when specimens of *kjerulfi* are prepared to reveal the interior (Pl. 83, figs. 1-4, 8-11), then the two species are seen to be very closely similar, although *B. kjerulfi* has a greater tendency to show lateral ribs. *B. kjerulfi* occurs in large numbers in restricted horizons at the very top of the Langåra Limestone-Shale Formation in the Asker area, particularly at Hvalsbakken, Grid Ref. NM 835350, and Semsvatnet, Grid Ref. NM 800364. The number of lateral ribs on either side of the median fold and sulcus varies within each sample from zero to four, with one or two being the most common. Kiaer (1902, pp. 65, 100) distinguished between a 'wide' and a'narrow' form, but there are specimens of intermediate width within each assemblage.

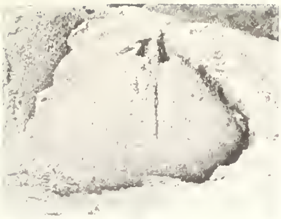
EXPLANATION OF PLATE 84

Figs. 1-11. *Thebesia scopulosa* sp. nov., all from 6 m below the top of the Langoyene Sandstone Formation, coast exposure on the south-west of Hovedoya, Oslo, Grid Ref. NM 968407. 1, 2, BB 70386, internal mould of a brachial valve and latex cast of it, ×4. 3, 4, BB 70400, internal mould of a pedicle valve and latex cast of it, ×4. 5-7, PMO 104.027, holotype, conjoined valves; in fig. 7 the brachial valve is uppermost, ×3. 8, 9, BB 70398, conjoined valves, ×4. 10, 11, BB 70399, conjoined valves, ×4.

Fig. 12. *Plectothyrella crassicostis* (Dalman, 1828), BB 71265, internal mould of a brachial valve, ×1·5, from 15 m above the base of the Langoyene Sandstone Formation, shore exposure at north-west Hovedøya, Oslo, Grid Ref. NM 965415.

Fig. 13. *Protatrypa* sp., BB 75306, conjoined valves viewed ventrally, ×3, from Husbergoya Shale Formation, 8 m from base of section at Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 854403.

Figs. 14-19. *Hindella cassidea* (Dalman, 1828), from within 2 m of the top of the Husbergøya Shale Formation, shore exposure at the western end of Langåra, Asker, Grid Ref. NM 856356. 14-16, BB 76156, three views of the internal mould of a pedicle valve, ×1·5. 17-19, BB 74880, three views of an articulated specimen, ×2.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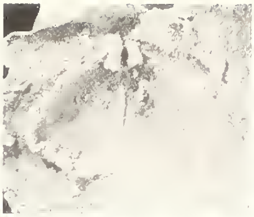
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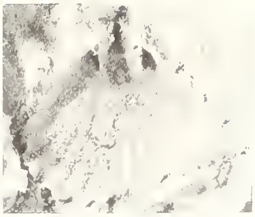
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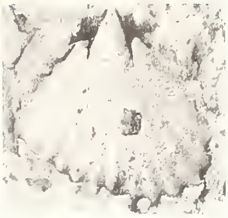
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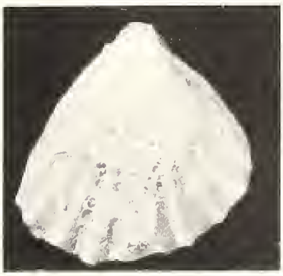
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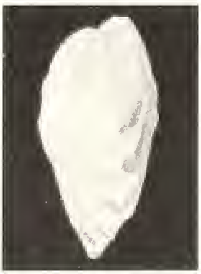
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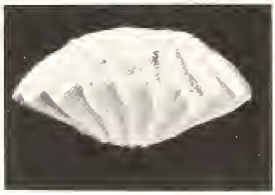
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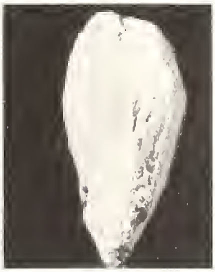
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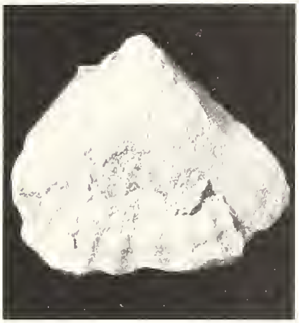
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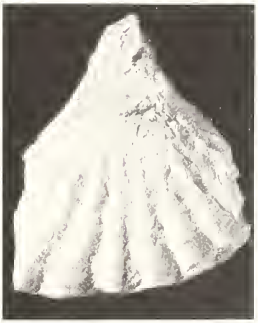
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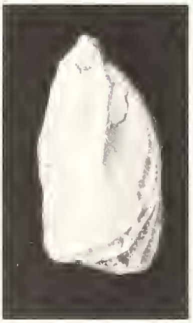
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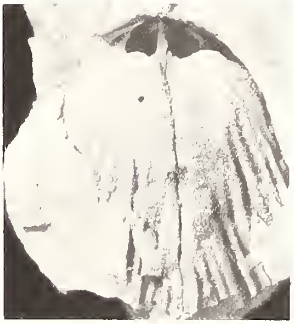
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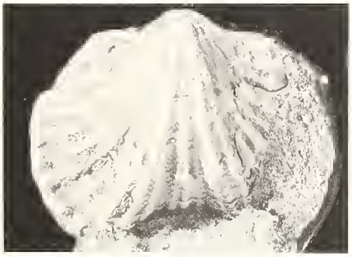
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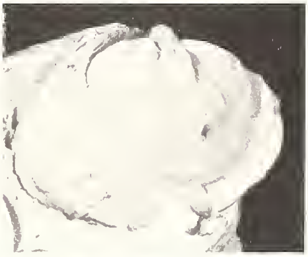
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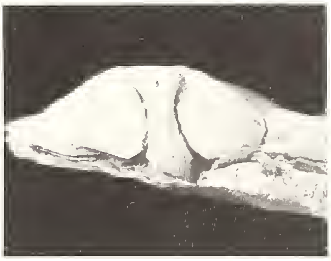
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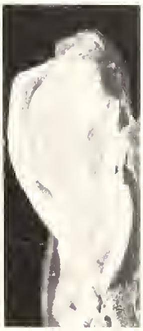
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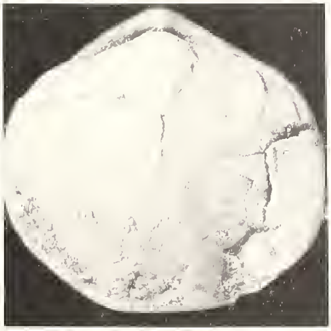
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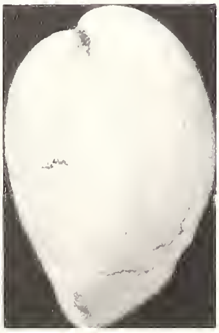
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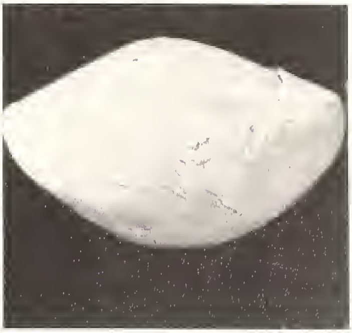
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COCKS, *Thebesia* and atrypoids

Order RHYNCHONELLIDA Kuhn, 1949

Rhynchonellides occur sporadically at several localities and horizons in the late Ashgill of the Oslo–Asker district, but, apart from the abundant *Thebesia* described below, they are never common enough to form more than a few per cent of the local assemblages. Forms identified include *Rostricellula*, *Stegerhynchus*?, and *Plectothyrella crassicostis* (Dalman, 1828), figured here in Plate 84, fig. 12; the latter is important elsewhere as a distinctive constituent of the *Hirnantia* community (e.g. Temple 1965; Bergström 1968).

Family TRIGONIRHYNCHIIDAE McLaren, 1965
Genus THEBESIA Amsden, 1974
Thebesia scopulosa sp. nov.

Plate 84, figs 1–11

Description. Exterior. Outline subtriangular, with prominent erect pedicle valve beak with relatively straight sides, which often curve anteriorly to become laterally concave in outline. Small but functional pedicle opening. Variable convexity, from nearly flat to fairly globose. About twelve ribs, difficult to count laterally since they merge with the flat shell sides; ribbing stronger anteriorly from about half valve length, the ribs curving gently antero-laterally. Anterior commissure usually fairly straight, but simple fold and sulcus sometimes weakly developed.

Pedicle valve interior. Teeth supported by well-developed but slender dental plates, subparallel on valve floor, but diverging slightly dorsally. Small transverse pedicle collar weakly developed at approximately the same distance anteriorly as the teeth. Muscle field not impressed.

Brachial valve interior. Cardinal process absent. Median septum present to half or two-thirds of the valve length. Prominent socket plates extend anteriorly to form crural bases, underneath which a small crurualium is present posteriorly. Indistinct suboval impressions of adductor muscle scars present on either side of the median septum.

Material. Holotype PMO 104.027 (Pl. 84, figs. 5–7), also BB 70379–70400, BB 76007–76056 from a channel fill near the top of the Langoyene Sandstone Formation, 6 m below the base of the Silurian at south-west Hovedøya, Oslo, Grid, Ref. NM 968408. The species also occurs abundantly in another channel fill 10 m further north and 5 m below the base of the Silurian (BB 70414–70147, BB 74823–74836). Occasional specimens doubtfully attributed to the species occur lower in the Langoyene Sandstone, for example BB 74327 from near its base at east Konglungen, Asker, Grid Ref. NM 850347.

Dimensions (in mm)	Length	Width	Thickness
PMO 104.027, conjoined valves, holotype	10·7	10·3	5·3
BB 70398, conjoined valves	7·4	6·4	4·4
BB 70399, conjoined valves	9·6	8·3	4·3
BB 76055, conjoined valves	8·2	9·3	4·0
BB 75974, conjoined valves	10·5	10·4	5·1

Discussion. Amsden's (1974) admirable redescription of the type species, *Thebesia thebesensis* (Foerste, 1909), leaves no doubt that the Norwegian material can be attributed to *Thebesia*. However, *T. scopulosa* reaches only two-thirds the size of *thebesensis*; it also differs in the occasional development of a slight sulcus, in the lesser divergence of the dental plates (compare Pl. 84, figs. 3 and 4 with Amsden (1974), pl. 14, fig. 1*e*), and in the relative proportions of the cruralium in the brachial valve. The mean perpendicular of the *T. thebesensis* points (in text-fig. 2) from the major axis based on the *T. scopulosa* plotted points was compared to zero using a normal deviate. The valve of the normal deviate was $-1{\cdot}63/0{\cdot}58$ (mean/standard error) $= 6{\cdot}3$. This is highly significant ($P < 0{\cdot}0001$), and indicates that there is a real difference in the growth patterns of the two species. One feature common to both species, and leading to its nineteenth-century identification for Norwegian specimens as '*R. cuneata*' on museum labels (e.g. on shells registered B 3899, presented by T. Kjerulf), is the elongate beak which tends to be concave laterally, a feature externally reminiscent of the true Silurian *Rhynchotreta*.

Order SPIRIFERIDA Waagen, 1883
Superfamily ATRYPACEA Gill, 1871

Atrypaceans occur rarely at several localities, but usually at scattered intervals through the rock, and there are not enought for systematic revision. Genera identified include *Zygospira*?, *Cyclospira*, *Eospirigerina*, and *Protatrypa* (Pl. 84, fig. 13).

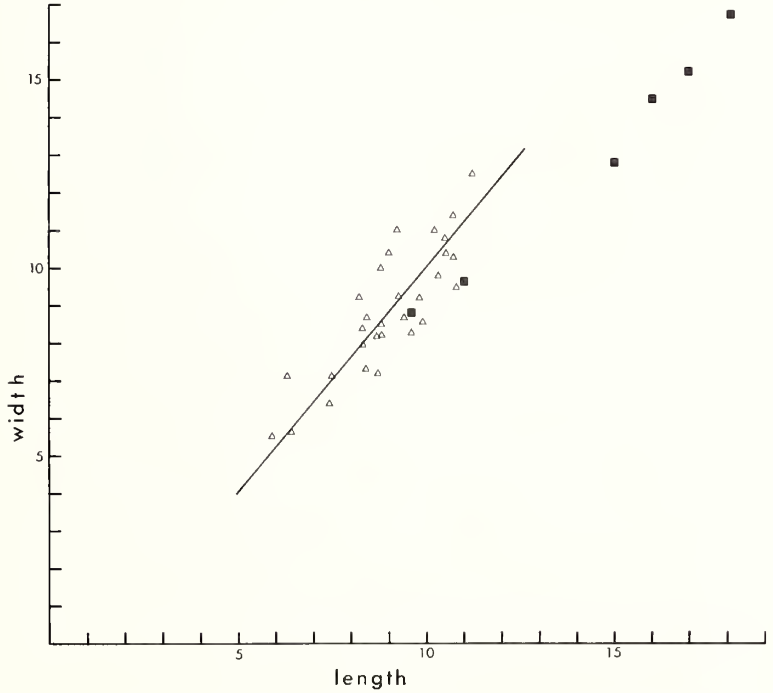
Superfamily ATHYRACEA M'Coy, 1844
Family MERISTELLIDAE Waagen, 1883
Genus HINDELLA Davidson, 1882
Hindella cassidea (Dalman, 1828)

Plate 84, figs. 14–19

1828 *Atrypa cassidea* Dalman, p. 134, pl. 5, fig. 5*a–d*.
1977 *Hindella cassidea* (Dalman); Sheehan, p. 29, pl. 1, figs. 1–25.
1977 *Hindella kiaeri* Sheehan, p. 37 *pars*, pl. 2, figs. 12–14, 16, 17, ?figs. 15, 18–22.

Material. In the Oslo–Asker district the species is common at a number of localities, for example in the Langåra Limestone-Shale Formation, particularly in and near the brown sandstone, e.g. at Langåra west (BB 74878–74886, BB 75250–75260), Grid Ref. NM 856356, and at Konglungen East (including BB 74330–74337), Grid Ref. NM 850347, and also in the Langoyene Sandstone Formation, for example in channel fills near the top of the formation at Hovedøya south (e.g. BB 76014–76031), Grid Ref. NM 968408.

Discussion. Sheehan (1977) has reviewed late Ordovician and early Silurian meristellids from Scandinavia, and redescribed Dalman's species *cassidea* from Borenshult, Ostergötland, Sweden.



TEXT-FIG. 2. Relative dimensions of *Thebesia scopulosa* in mm from Hovedoya, Oslo (open triangles), and *Thebesia thebesensis* from Illinois and Missouri, USA (black squares); the American data from Amsden (1974, p. 90). The reduced major axis for the Norwegian sample is also shown.

Sheehan also described a new species, *H. kiaeri*, partly on material showing only the exterior (including the holotype) from the late Ashgill of Nesoya, Oslo–Asker region, and partly on material including internal moulds from the early Llandovery of Baerum. Sheehan (1977, p. 38) lists five differences between *H. cassidea* and *H. kiaeri*: four of these are internal differences (based on the early Llandovery material), and the fifth is the 'more inflated shell' of *H. kiaeri*. *Hindella* is common in the late Ashgill of the Oslo–Asker district, and is clearly attributable to *H. cassidea*, including a wide range of shell shapes intergrading between *H. cassidea* and *H. kiaeri*. Internally the Oslo–Asker forms appear identical to *H. cassidea* (e.g. Pl. 84, figs. 14–16), and they are all identified as that species here, including topotype specimens of *H. kiaeri* (BB 75364–75366). Whether or not the early Llandovery forms ascribed to *H. kiaeri* are different from *H. crassa* (J. de C. Sowerby, 1839) requires further investigation; and if so they would require a new name.

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ECOLOGICAL ASSOCIATIONS IN A REGRESSIVE SEQUENCE: THE LATEST ORDOVICIAN OF THE OSLO-ASKER DISTRICT, NORWAY

by P. J. BRENCHLEY *and* L. R. M. COCKS

ABSTRACT. Ten faunal associations are defined and documented from numerous collections made in the late Ashgill rocks of the Oslo-Asker district, Norway. The distribution of the associations is integrated with previous work on the sedimentology which demonstrated a regressive sequence caused by the eustatic fall in sea level due to the end-Ordovician glacial event. The associations in late Rawtheyan times were a *Tretaspis* Association in the deeper shelf, with an *Onniella* Association midshelf, which was also colonized in places by *Palaeoporella* thickets and by cystoids. The *Onniella* Association persisted into Hirnantian times, with the *Hirnantia* Association *sensu stricto* situated up-slope from it. Shallower still were the *Dalmanella*, *Hindella-Cliftonia*, and *Holorhynchus* Associations, with other associations dominated by bivalves and *Monocraterion* inhabiting the lower shoreface. More specialized *Thebesia* and *Brevilamnulella* Associations are also recognized, which colonized tidal channels and ooidal shoals at the top of the Ashgill sequence. The area was subsequently blanketed by the early Silurian transgressive deposits containing at their base specialized shelly faunas and then shales with graptolites, some of which can be attributed to the early Llandovery *acuminatus* Zone.

LATE Ordovician faunas in the Oslo-Asker district of Norway are found within a well-marked regressive sequence (Brenchley and Newall 1975) which provides an excellent framework in which to study the nature of the faunal associations and their environmental distribution. In spite of the fact that our locality collections tend to contain a small number of individuals, they are rich in species and it is possible to recognize recurrent associations which occur in consistent sequence in many laterally equivalent successions and apparently reflect a spectrum of environmentally controlled animal communities.

The vertical sequence of fossil associations can be related to a sequence of sedimentary facies, starting with mudstones of an open-shelf environment passing through various facies of the shoreface, and ending with oolite shoal and tidal channel facies. However, as well as the vertical arrangement of fossil associations there are also lateral changes in the fauna which are probably related to an Ordovician palaeoslope which declined eastwards from the Asker district towards the Oslo district. These lateral changes in fauna can be inferred because there are some distinctive lithological horizons, believed to be synchronous, which can be traced throughout most of the area, and thus enable us to establish some lines of correlation which are independent of the fauna.

Towards the end of the Ordovician there was an episode of extinction affecting several fossil groups (Newell 1967; Paul 1976; Rickards 1978) which caused a discontinuity between Ordovician and Silurian faunas, particularly in North America. This discontinuity has been related to lowered sea level associated with the end-Ordovician glaciation of 'Gondwanaland' (Sheehan 1973; Berry and Boucot 1973). Many late Ordovician faunas have a low diversity and are commonly represented by a single *Hirnantia* fauna which might possibly be associated with widespread cold surface waters (Sheehan 1979). However, some, possibly lower latitude, Hirnantian faunas can be relatively diverse (Bergström 1968; Williams and Wright 1981). The Hirnantian rocks of the Oslo-Asker district are believed to have formed in sub-tropical latitudes and contain faunas which are not only diverse but occur in several distinct associations.

This paper describes the late Ordovician associations, relates them to vertical and lateral environmental changes, and discusses the extent to which late Ordovician warmer water associations are modified by contemporaneous glacio-eustatic sea level changes.

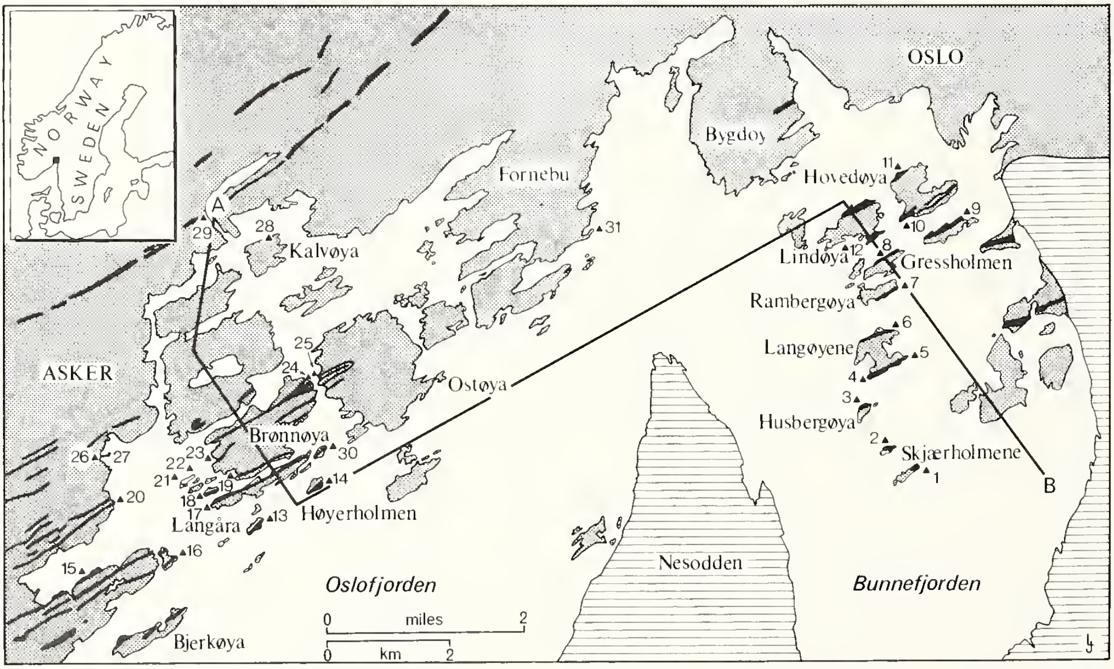
[Palaeontology, Vol. 25, Part 4, 1982, pp. 783-815, pls. 85-86.]

STRATIGRAPHICAL FRAMEWORK

Upper Ordovician rocks are repeatedly seen on the flanks of tight north-east- to south-west-trending folds in the Oslo–Asker district. The complete upper Ordovician sequence, described by Brenchley and Newall (1975), is seen at nearly thirty localities on the shores of the islands in the Oslofjord and the Bunnefjord and there are other less complete sequences exposed inland (text-fig. 1, localities 1–31). Faunas have been collected from nineteen of these sections (text-fig. 3) and the distribution of the fauna has been noted in all the others.

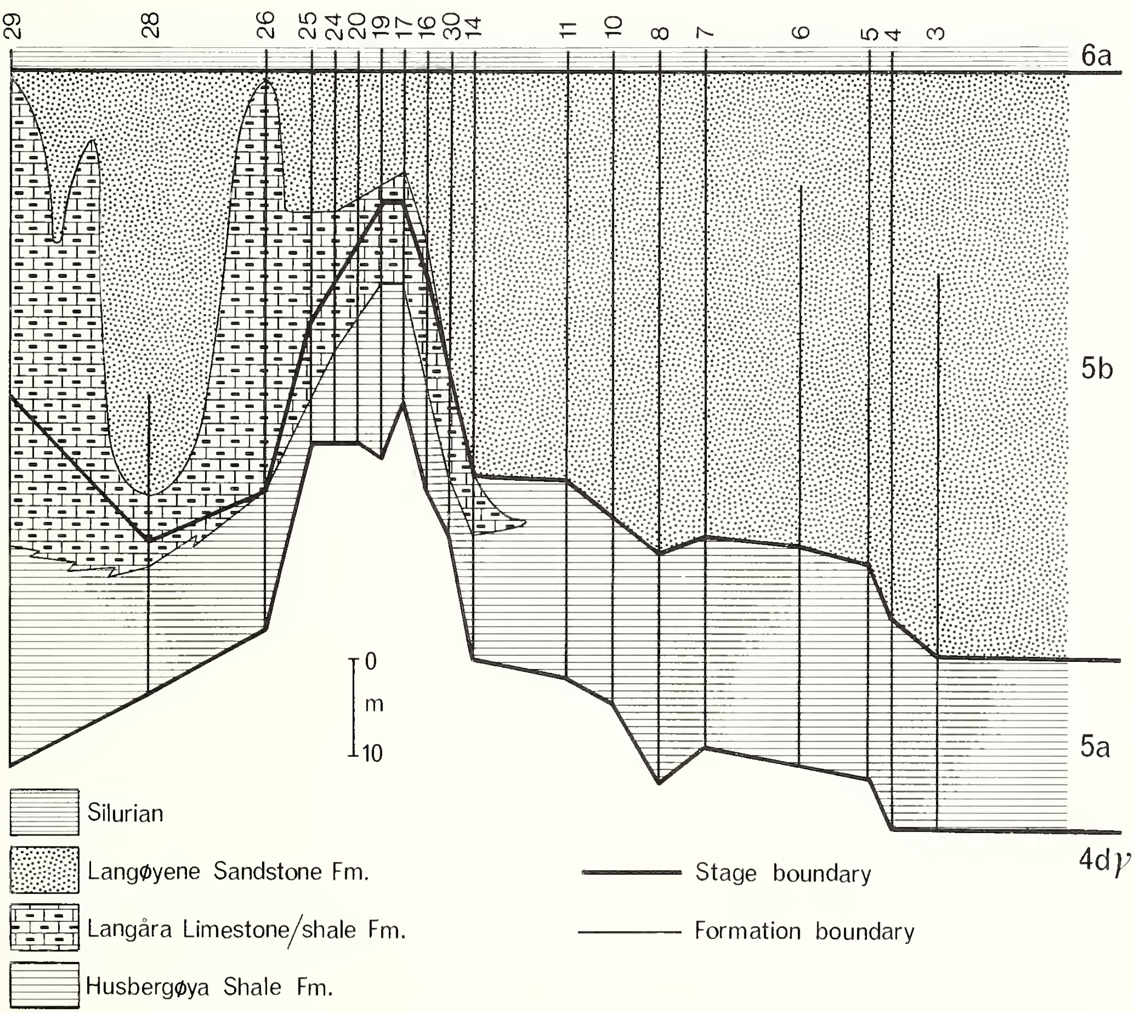
The upper Ordovician rocks of the area occur as three formations, with a lower Husbergoya Shale followed by two laterally equivalent formations, the Langoyene Sandstone in the east and the Langåra Limestone–Shale Formation in the west. There is, however, some intertonguing of the three formations in the middle part of the area (text-fig. 2). We have modified the stratigraphical profile shown in figure 3 of Brenchley and Newall (1975) to emphasize the deep erosion and channelling which is found in the north-west part of the area. The mainly coarse-grained sediments which fill the channels have been included within the Langøyene Sandstone Formation.

We have found it useful to continue using, in an informal way, the long-established Norwegian Etasjer, even though Owen (1978) and Bruton and Owen (1979) have recommended that their use be discontinued. Initially the Etasjer were based on lithostratigraphical criteria, though later they were given chronostratigraphical status (Code of Stratigraphical Nomenclature for Norway, 1969). The upper Ordovician Etasjer are shale/nodular limestone rhythms chiefly from 10 to 50 m thick. They are clearly developed within the Oslo–Asker district but cannot be correlated more widely, so there appears little justification for more than their local use. However, because the rhythm boundaries reflect changes in deposition from suspension of mainly argillaceous material in a shelf environment it is possible that the boundaries are synchronous throughout the local area (but see Bruton and



TEXT-FIG. 1. Locality map showing the position of the principal sections through Stage 5 in the Oslo–Asker district. The Precambrian is shown with horizontal shading, the Lower Palaeozoic with stipple, and Stage 5 is shown black. The line A–B shows the position of the stratigraphic profiles shown in text-figs. 3, 7, and 8.

Owen 1979 for an alternative view). This suggestion is supported, as far as the Stage *5a* boundaries are concerned, by the precise lithological similarity of the Stage *5a* sequences in the Oslo–Asker district from section 3 to section 25 in text-fig. 2. Each section shows a sharp change at its base from the nodular limestones of *4dγ* to the shales of *5a*, and contains a very distinctive development of large spreiten-bearing ichnofossils (Pl. 85, fig. 5) particularly cf. *Trichophycus* (Seilacher and Meischner 1965) about 3 m above the base. Interbedded with the succeeding shales are thin sandstones deposited from storm-generated currents which reach their peak frequency at a level between 40% and 60% up the sequence, but are always absent in the top 10–20% of the sequence (Brenchley, Newall and Stanistreet 1979). Finally, the top 1–3 m is always a bioturbated very fine brownish-weathering sandstone, characteristically containing cystoids. These features occur so consistently in each section that we believe they are good evidence for the synchroneity of each lithological horizon. The correlation so established allows the recognition of the Stage *5a*/*5b* boundary in the mid-western sections, where the Langåra Limestone–Shale Formation is developed as a lateral equivalent to the upper part of the Husbergøya Shale (text-fig. 2).



TEXT-FIG. 2. Stratigraphical profile from north-west to south-east across the Oslo–Asker area. The numbered vertical lines refer to the measured sections shown in text-fig. 1.

Although it is possible to recognize the $4d\gamma/5a$ boundary throughout the whole of the study area, there are subtle changes in facies towards the north-west, and neither the distinctive spreiten-bearing trace fossil horizon nor the cystoid-bearing sandstone can be traced north-westwards of locality 25. Consequently the top of the *5a* cycle cannot be located with confidence, but we have tentatively placed it 2 m above the last thin sheet sandstone in the section to conform with other sections in the Asker district. Since the faunas on this north-west part of the area are also different from those to the south-east and lack both the stratigraphically valuable *Tretaspis* fauna and the *Hirnantia* fauna, it is not possible to make a firm correlation there on biostratigraphical evidence.

Throughout most of the area the faunas provide a basis for correlation with the type Ashgill sequence in Britain. The Husbergøya Shale has *T. sortita broeggeri* widespread in the topmost few metres of the formation, which Owen (1980) regarded as indicative of the topmost part of the Rawtheyan Stage. Since *Tretaspis* disappears within the bioturbated sandstone at the top of the Husbergøya Shale and is absent in the shales at the base of the overlying Langøyene Formation, it appears likely that this disappearance is of stratigraphical rather than of ecological significance. In Britain *Tretaspis* disappears abruptly at the top of the Rawtheyan (Ingham 1966). This placing of the Rawtheyan/Hirnantian boundary within a few centimetres of the top of the Husbergøya Shale is supported by the first appearance of a *Hirnantia* fauna at one locality in the uppermost few centimetres of the Formation, and the appearance more generally of that fauna in the lowermost few metres of the Langøyene Sandstone.

The relatively sparse faunas at the top of the Langøyene Sandstone Formation do not provide a basis for correlating this part of the sequence. However, the overlying shales contain graptolites, and have yielded a fauna from a locality 11 m above their base indicative of the lower *acuminatus* Zone (Howe 1982). This suggests that the upper boundary of the Langøyene Sandstone Formation probably lies within the *persculptus* Zone.

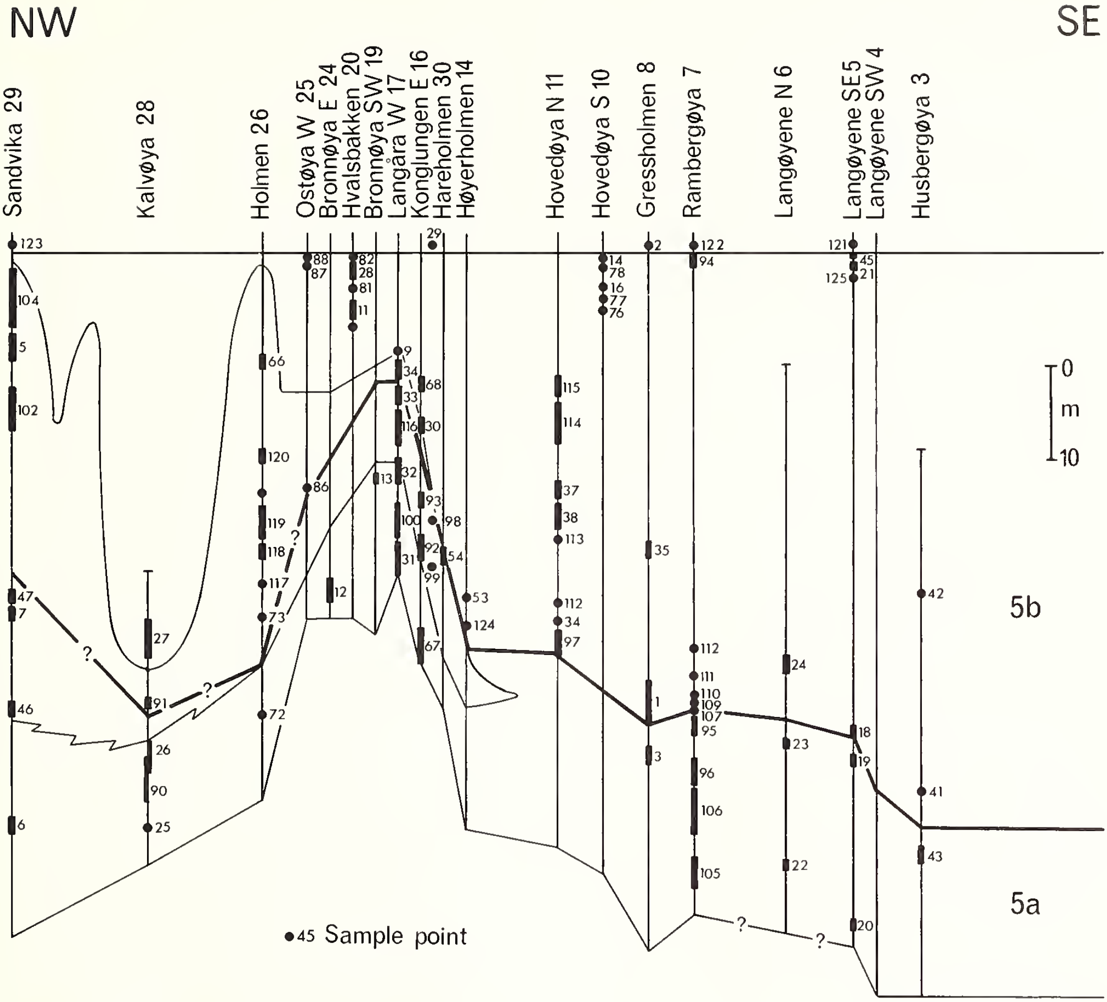
TERMINOLOGY AND SAMPLING METHODS

Throughout this account we have used the term ‘assemblage’ to mean the collected sample; ‘association’ refers to the recurrent association of taxa in a group of assemblages; and a ‘community’ is regarded as a biological association of taxa usually related to particular environmental conditions (Pickerill and Brenchley 1975).

The fossil assemblages described in this paper come mainly from argillaceous sediments, though a small proportion come from arenaceous sediments of the Langøyene Sandstone Formation. The fossils in the argillaceous sediments are generally disseminated through the bioturbated grey, calcareous silty mudstones of the Husbergøya Shale, the Langåra Limestone-Shale, or the lower part of the Langøyene Sandstone Formation, or may be found in the interbedded calcareous nodules or limestone beds of the last two units. Interbedded with the shales are thin sandstones, but these rarely contain fossils, and there are also a few thin bioclastic limestones in the west of the area which can be relatively fossiliferous. Most of the fossils occur individually rather than in clusters, though a few life assemblage clusters are recorded, and most fossils lie at variable angles to the bedding. Bedding plane samples are relatively rare. The faunas, though sparse, are diverse and include variable proportions of trilobites, brachiopods, bryozoans, gastropods, corals, orthocone nautiloids, etc. The trilobites usually occur as fragments, the gastropods and orthocones are often complete, whilst the brachiopods are commonly represented by some articulated valves in any one assemblage.

Disturbance of the shells prior to fossilization could have been the result of deep storm waves, wind-driven bottom currents, or bioturbation of the sediment. Bottom currents would have sorted the shell material into layers and produced bedding plane assemblages, so we believe the dispersed occurrence and variable orientation of the shells is possibly the result of wave stirring, but accentuated by the activity of burrowing organisms. We therefore regard most of the assemblages as essentially untransported or at most ‘disturbed neighbourhood assemblages’ (Scott 1974).

However, there are two groups of samples where shells may have been significantly moved, even though they are still indigenous to the area. In a few assemblages of the *Dalmanella* and *Hindella-Cliftonia* Associations, brachiopods, corals, and *Tentaculites* occur in thin- to thick-bedded sandstones representing a shoreface

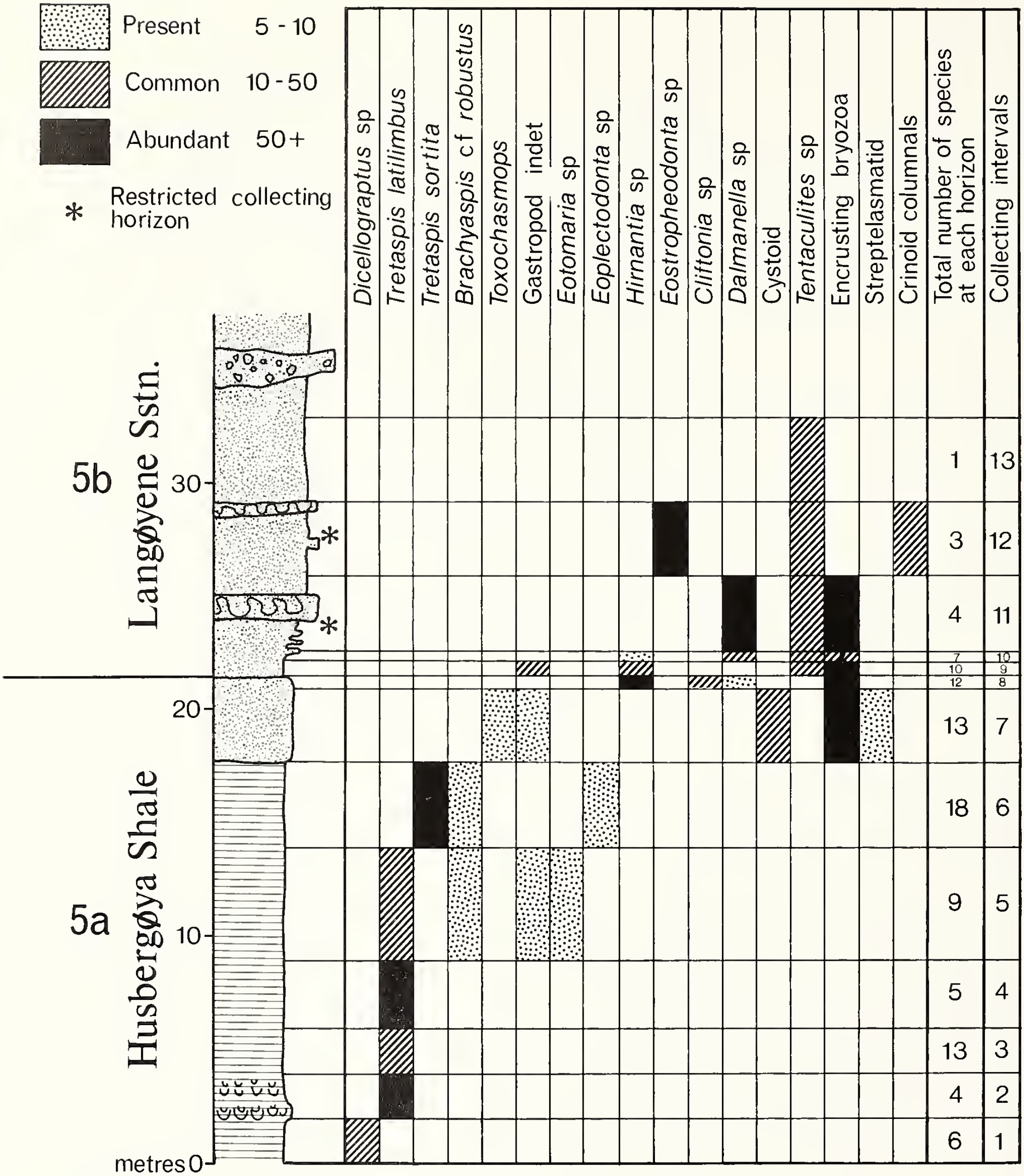


TEXT-FIG. 3. Stratigraphical profile from north-west to south-east across the Oslo-Asker area showing the position of the collections described in the text and Tables.

environment. However, most of the *Dalmanella* shells are articulated and are therefore unlikely to have travelled far, but these assemblages might be regarded as transported assemblages of local origin.

In other cases, fossils occur near the top of the tidal channel facies at Hovedøya (section 10) and in bioclastic coquinas at Hvalsbakken (section 20): the brachiopod valves are disarticulated and the faunas are clearly transported, but the dense accumulation of unbroken shells chiefly consisting of one or two dominant species suggests that the assemblage is indigenous to the area. In contrast, conglomeratic sediments filling the tidal channels have abraded corals and fossiliferous limestone clasts which are clearly allochthonous, and we have not considered these faunas in this account.

The very low density of fossils at most levels in the succession and the rarity of bedding plane assemblages has influenced our sampling methods. Bulk samples of a practical size (2–5 kg) have yielded very few fossils from these Ashgill sequences and therefore provide an incomplete sample of the fauna. Even persistent collecting from the outcrop has frequently yielded small samples which may be inadequate even to identify several of the taxa present. As an example, text-fig. 4 shows the results of collecting from the outcrop for two man hours per horizon in one section at Rambergøya. The thirty-four metres of the section yielded approximately fifty taxa, but of



TEXT-FIG. 4. The stratigraphical sequence at Rambergøya (section 7) showing the distribution of the commoner elements of the fauna in the sequence, and the diversity at each collecting interval.

these only six taxa occurred with more than fifty individuals within any one horizon, five other taxa were represented by between ten and fifty individuals, whilst all the other taxa yielded fewer than ten specimens. Note that in the Husbergøya Shale, in spite of a diversity as high as eighteen species per horizon, only *Tretaspis*, and at one horizon bryozoa, occurred as more than ten specimens. We have found that the ease with which fossils can be collected through the sequence is variable. This sometimes reflects the presence of a larger number of fossils but it also partially reflects the ease of collecting from the outcrop and the degree to which the shales have been decalcified. We have collected these relatively productive horizons (text-fig. 3) intensely, to a point where we find further collecting does not appear to significantly change the composition of the fauna, though we are aware that with such diverse assemblages further species are probably present. We have recorded field observations of the fauna in all the sections shown in text-figs. 2 and 3 to ensure that the less fossiliferous parts of the section are not found to contain a different fauna from that at the more richly fossiliferous levels. Further, we have systematically collected through two sections (7 and 17) to determine more rigorously whether our 'spot samples' were representative of broader stratigraphical levels. In nearly every case the spot samples contain the same fauna as the adjacent beds but are richer and have additional species. We therefore believe that the faunas from the sample-points shown on text-fig. 3 are a good reflection of the preserved biota, and may be used to analyse changing taxonomic composition and diversity in the succession.

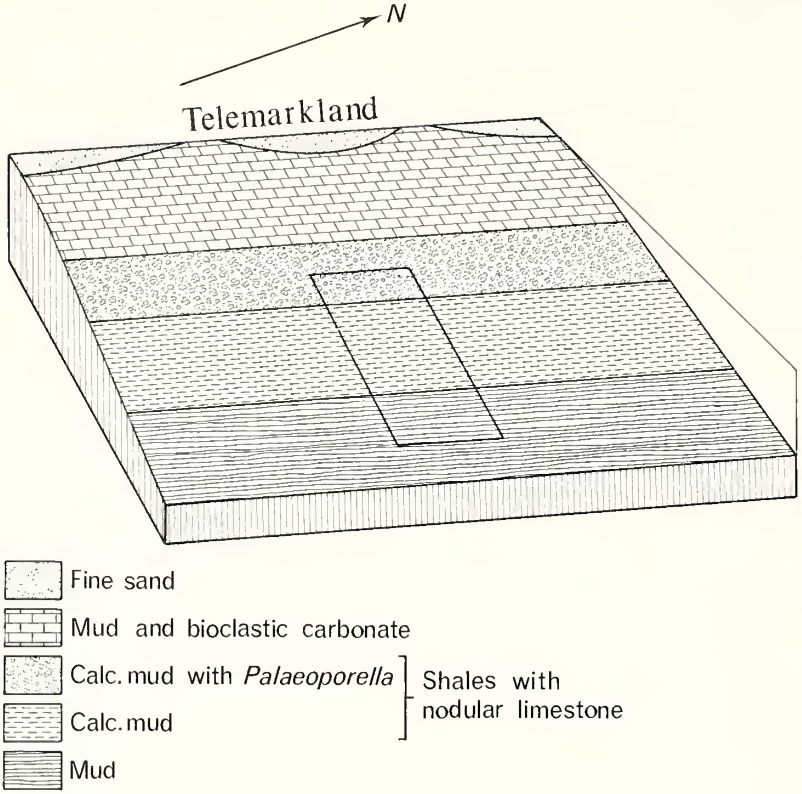
Samples collected in vertical sequence are analogous to the line transects used by modern ecologists (Djörjes 1971; 1972). Histograms of faunal distribution through vertical sequences have been used (e.g. by Hurst 1979*a*, *b*; Watkins 1979; Lockley 1980) to recognize major changes of fauna within a sequence and hence to define faunal associations. We have used the same principles in recognizing faunal associations in the Oslo region but, because of the relatively small size of many of the samples, and because some distinctive faunas are very restricted in their vertical distribution and have been collected as a single assemblage from a metre or two of section, it is inappropriate to plot the data in the form of histograms. We have instead presented them as a series of Tables (1–9) which show the common species and their abundance in each association.

Because we have been selective in our choice of samples, and have been unable to collect samples of the same size, we are unable to make quantitative statements about the density of faunas through the sequence, though an impression of varying density can be gained from text-fig. 4. The absolute values for the diversity of the assemblages are similarly affected by our sampling and should be used as a guide to the relative diversity of the assemblages.

In palaeoecological studies it is important to be aware of the limitations imposed on any conclusions by the nature of the sampling. The practical target population (Krumbein 1960) in palaeoecology is at its broadest 'the preserved part of the former biota'. However, the actual choice of target population depends upon the aims of the study. The aim may be to study the environmental distribution of a whole biofacies, or a particular group of fossils, it may be to test ecological theories of diversity, colonization, or equilibrium, or to make comparative studies of communities at different stratigraphical levels. The most commonly selected targets are 'the entire preserved biota' (e.g. Watkins 1979; Jaanusson, Laufeld and Sköglund 1979), or the preserved part of a single taxonomic group such as brachiopods or bryozoa (e.g. Williams 1976; Ross 1970), or the occurrence of individual genera or species (e.g. Broadhurst and Worsley 1975; Hurst 1978). Studies which restrict the target population often gain from more effective sampling, but lose by the restricted scope of the conclusions. We have selected the 'entire preserved biota' (apart from microfossils) as the target population, but we believe that brachiopods and trilobites are particularly well represented and identified in our faunal lists, whereas, for example, ostracodes are under-recorded, although we have tried to overcome this deficiency where possible by enlisting the aid of other specialists. It has not been possible to compare the completeness of our faunal records with previous lists because there are relatively few collections described from Stage 5 rocks in the Oslo–Asker district, and most of those that have been described are based on rather poorly localized museum collections. The taxonomy of fossils from the Oslo–Asker area is still under-studied, but Kiaer (1902) and Wright (1965) have recorded some brachiopods, Kiaer (1899), Wedekind (1927), Spjeldnaes (1964), and Neuman (1969) some corals, Strand (1934) has described the cephalopods, and the ostracodes were described by Henningsmoen (1954). The proetid trilobites were described by Owens (1970), and most of the other trilobites by Owen (1980; 1981). The echinoderms are being studied by Bockelie (in press) whilst the commoner elements of the brachiopod fauna are described in an accompanying paper (Cocks 1982). The authors of the species quoted may be found in these works. In this paper we take the term 'diversity' simply to mean the number of different taxa present in a collection from a single bedding plane.

Thus, we believe that the identifications of the commoner brachiopods and trilobites are sufficiently accurate to make conclusions about changes in the taxonomic composition and diversity of the assemblages, whereas the less precise information on the rest of the faunas allows the recognition of biofacies and broad changes in diversity, but does not allow conclusions about the detailed ecology of the communities.

The collections, apart from the brachiopods, are housed in the Paleontologisk Museum, Oslo and the holotypes of the new brachiopod species (described in Cocks 1982) are also stored there. The main part of the brachiopod fauna is stored in the British Museum (Natural History).

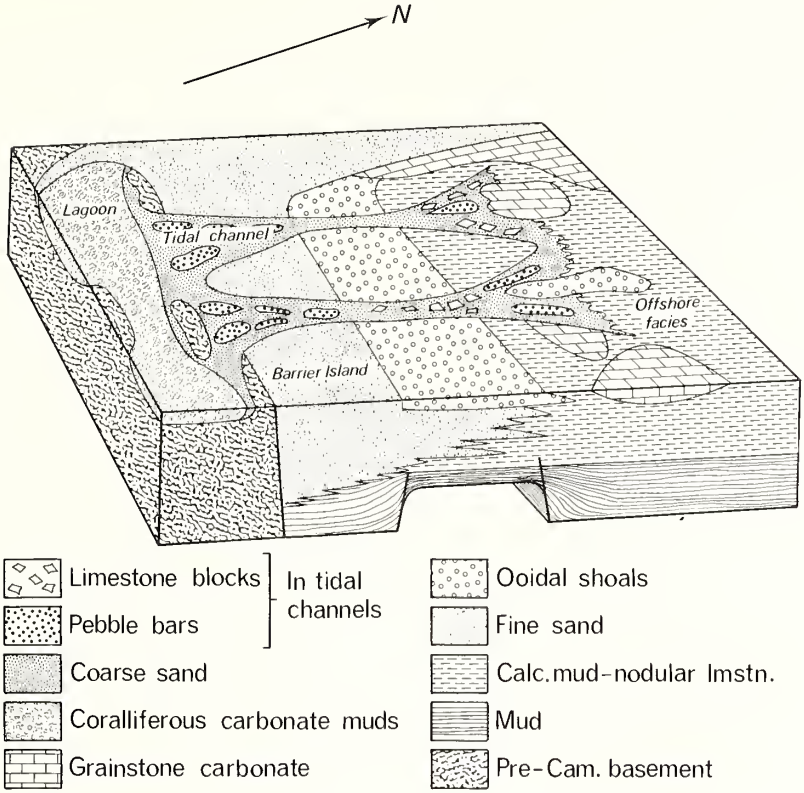

N
Telemarkland
Fine sand
Mud and bioclastic carbonate
Calc. mud with *Palaeoporella*
Calc. mud
Mud
Shales with nodular limestone

TEXT-FIG. 5. A reconstruction of the palaeogeography of the Oslo region in Stage 5*a* (late Rawtheyan) times. The rectangular grid approximately outlines the study area, which measures about 24 km by 16 km.

PALAEOGEOGRAPHICAL SETTING

The palaeogeography of the area in late Rawtheyan (Stage 5*a*) and earliest Hirnantian times consisted of fairly deep-shelf muddy environments established on a low eastward-facing palaeoslope (text-fig. 5). Into this low-energy environment storm-generated currents swept sand on rare occasions to form sheet sandstone beds within the generally argillaceous succession (Brenchley *et al*. 1979). The muddy sediments were more calcareous towards shore and this led to the development of the visually striking nodular limestones of the Langåra Limestone–Shale Formation. The nodules are diagenetic in origin but may reflect an originally higher content of biogenic carbonate mud within the sediment. The principal substrate throughout the area was silty mud and this is unlikely to have exerted a strong control on the ecology unless there were marked differences in its cohesion.

Soon after the start of Hirnantian times there were radical changes in the palaeogeography, which were probably initiated by differential block movement within the region, but emphasized by the significant late Ordovician glacio-eustatic regression. The early Hirnantian fault movements appear to have produced a tectonic high with a new ENE–WSW orientation (text-fig. 6), along which barrier islands became established with a seaward-facing shoreface towards the north. The sediments of the shoreface, of tidal channels, of oolite shales, and of the more offshore facies (text-fig. 6) are all well



TEXT-FIG. 6. A reconstruction of the palaeogeography of the Oslo region in Stage 5*b* (mid Hirnantian) times. Note the realignment of the facies belts along an ENE-WSW trend.

exposed in regressive sequence in the Oslo-Asker district, but the presence of land and lagoons along the tectonic high is deduced from the sediment transported into the tidal channels and preserved in the study area.

At the close of the Ordovician the palaeogeography changed once more. The rise of sea level which resulted from the initial melting phase of the Gondwana ice cap rapidly drowned the varied late Ordovician shallow marine facies and left a veneer of transgressive sediment followed by muds of a deep-shelf environment (Brenchley and Newall 1980). Following the transgression the regional eastward-facing palaeoslope was established once again and remained stable throughout at least the early part of Silurian times.

The faunal associations described in the following sections are related to the three phases of palaeogeographical development. The *Tretaspis* Association, *Onniella* Association, *Hirnantia* Association, *Hindella-Cliftonia* Association, and *Dalmanella* Association are all developed on the regional eastward-facing palaeoslope in Rawtheyan and early Hirnantian times. However, some *Hirnantia* assemblages are found in the shoreface sediments related to the later Hirnantian palaeogeography, and the *Holorhynchus* Association, *Thebesia* Association, *Brevilamnulella* Association, and *Monocraterion* Association are all related to this new palaeogeography. Finally, there are a small number of assemblages related to the end-Ordovician transgression.

THE FAUNAL ASSOCIATIONS

The Tretaspis *Association* (Table 1)

The association occurs as very sparse but moderately diverse assemblages dispersed through the mudstones of the Husbergøya Shale Formation. *Tretaspis* is consistently the commonest fossil and is represented by *T. latilimbus norvegicus*, except in the topmost three metres or so of the Husbergøya Shale, where *T. sortita broeggeri* (Pl. 86, fig. 1) is found. *Toxochasmops* sp., *Stygina latifrons extensa* (Pl. 86, fig. 5), and calymenid species are found in several assemblages and a total of at least twelve species of trilobite are found in assemblages assigned to this association (Table 1). In addition to trilobites there are several species of gastropods, of which loxonemataceans are the most common, and at least two bivalve genera are present. Bryozoa occur sporadically and in small numbers. The trace fossil *Chondrites* is ubiquitous and at a horizon low in the Husbergøya Shales there is a distinctive large trace fossil with spreiten (Pl. 85, fig. 5), referred to by Seilacher and Meischner (1965) as *Trichophycus*. Brachiopods are generally few in number and mainly occur in the middle and upper

TABLE 1. The *Tretaspis* Association. In this and the ensuing Tables 2–9 the numbers of specimens from each locality are shown. In animals with more than one fossil part, only the number of the more abundant part is included; for example, if 25 pedicle valves and 19 brachial valves of the same brachiopod species were found, then 25 would be shown in the table. The diversity simply indicates the total number of different species in a single collection. The numbers after each taxon in the 'Associated fauna' refer to the number of localities at which each was found: the absence of a number means that it was found at only one locality. Trace fossils and crinoid ossicles were not included in the counts. The localities are as shown on text-fig. 3.

	Localities											
	20	105	23	19	43	36	3	106	6	7	40	22
Trilobites												
Tretaspis latilimbus norvegicus	3	9						12	5		5	2
T. sortita broeggeri			5	5	10	4	5			5		
Toxochasmops sp.			1		1	1	1		2	1		
Stygina cf. *latifrons extensa*				2			2	1		1		
calymenid					1			2	2	2	3	
Brachiopods												
Eoplectodonta oscitanda			3					3	3			4
Others												
loxonemataceans			5				6		3	2		
thin stick trepostomes				10+						8		2
Total number of specimens	4	12	19	22+	13	5	19	23	23	31	9	12
Diversity	2	4	9	6	4	2	8	7	11	13	3	5

Associated fauna includes:

Trilobites: *Brachyaspis* cf. *robustus* (2), *Cybeloides* sp., *Dionide* sp., *Dicranopeltis* aff. *polytoma*, *Lonchodomas* sp., *Sphaerocoryphe* sp., *Primaspis bucculenta* (2).

Brachiopods: *Epitomyonia* sp., *Leangella* sp., *Leptaena* sp., *Onniella kalvoya* (2), orthid indet., rhynchonellid? indet., *Strophomena*? sp., *Orbiculoidea* sp. porambonitacean?

Molluscs: bellerophontaceans (2), *Cymbularia pachygaster*, *Eotomaria* sp. aff. *eotomaria*, *Holopea*? sp. (2), *Palaeoneilo*? sp., *Praenucula*? sp.

Others: fenestellid bryozoa, *Serpulites* sp., *Climacograptus* sp.

Crinoid ossicles are rare.

Trace fossils include the ubiquitous *Chondrites* sp. *and Trichophycus*? sp.

Average number of specimens per locality: 16·0.

Mean diversity: 6·2.

part of the sequence containing the *Tretaspis* Association. The most characteristic brachiopod is *Eoplectodonta oscitanda*, but *Onniella kalvoya* is also recorded. These species are more typical of the *Onniella* Association (described below) and we regard some assemblages in the upper part of the Husbergøya Shale, where these species are more common, as belonging to a mixed *Tretaspis–Onniella* Association (see text-fig. 5).

Two species of cystoid, *Tetreucystis* sp. and *Eucystis* sp. (Bockelie, in press), are found in a bioturbated sandstone at the top of the Husbergoya Shale. This horizon is distinctive and we informally refer to it as the cystoid bed. The associated fauna belongs to the *Tretaspis–Onniella* Association.

The diversity of the assemblages in the *Tretaspis* Association is only moderate, but relative to the number of specimens collected is often high. From field observations we have found a maximum of eighteen taxa from one horizon (horizon 6, text-fig. 4). Samples collected from all the localities in the association, often from over ten man-hours' collecting, have yielded an average of 6·2 taxa from an average sample of 16·2 individual specimens.

The brachiopods in the *Tretaspis* Association are generally found both articulated and disarticulated and the trilobites are fragmentary. The fact that the fossils are found dispersed in the mudstones and are not sorted into layers indicates that they have probably not been transported, and it therefore seems likely that the fauna of the *Tretaspis* Association lived in the environment in which it is found, but that it might have been periodically disturbed by deep waves or transient bottom currents such as are recorded from modern continental shelves (e.g. Komar, Neudeck and Kulm 1972; Mooers 1976). Many of the fossils have also been disturbed by post-depositional organic activity, evident in the extensive bioturbation of the sediment.

The relative abundance of trilobites and gastropods and the ubiquitous presence of *Chondrites* in the association indicates a predominance of deposit-feeders amongst the preserved part of the fauna. However, filter-feeders are thinly represented by occasional brachiopods, crinoids, and bryozoa.

Stratigraphically the association occurs throughout most of the Husbergøya Shale, though there are some small changes in the fauna upwards through the sequence. In the lowermost two metres of the formation shelly faunas are rare or absent and instead diplograptids are found at a few localities. In the succeeding beds there is a sparse but diverse trilobite fauna and, above this, first brachiopods and then cystoids become successively more common, suggesting a slight progressive shallowing. The passage from beds with graptolites into beds with the *Tretaspis* Association indicates that the latter is at the deep end of the spectrum of benthic faunas. This conclusion is supported by the presence of the *Tretaspis* Association only in the east of the study area, whilst a richer, more varied fauna occurs at the same stratigraphical horizon in the west, which according to palaeogeographical interpretations was higher up the regional palaeoslope (Brenchley *et al.* 1979).

The Onniella *Association* (Table 2)

The *Onniella* Association is generally a low-density, high-diversity association and occurs as assemblages rather sparsely dispersed through the shales and nodular limestones of the Langåra Limestone–Shale Formation. The commonest elements of the fauna are brachiopods, but bryozoa are present in most assemblages and both simple rugose and tabulate corals are commonly present but rarely in abundance.

The characteristic brachiopods are *O. kalvoya* and *E. oscitanda*, which are each present in fourteen out of the fifteen assemblages included in the association. *Nicolella* sp. and *Leptaena* sp. are commonly present in small numbers and a thick stick bryozoan resembling '*Hallopora*' and hemispherical encrusting bryozoa are present in many localities. *Triplesia* sp., *Dolerorthis* sp., and *Sampo* sp. are found particularly in assemblages low in the stratigraphical sequence, while *Eospirigerina* is more common higher in the sequence. *Glyptorthis* sp., *Sampo* sp., *Orthambonites* sp., *Oxoplecia* sp., and *Platystrophia* sp. are moderately frequently found throughout the whole range of assemblages. Forty-eight genera of brachiopods have been recorded, but many of these are found only in small numbers at a few localities.

TABLE 2. The *Onniella* Association

	Localities														
	31	67	12	25	75	72	26	32	6	7	27	46	47	48	73
Brachiopods															
Onniella kalvoya	8	3	46	14		1	11	6	14	17	24	5	1	19	8
Eoplectodonta oscitanda	5	1	4	2	1		16	3	5	3	2	4	3	6	2
Nicolella sp.	3	3	1	2		1	1		3	6		2		5	8
Leptaena sp.	2		6	4		1			2	1	5	1	2	2	5
Triplesia sp.	8	1	7						1			1			1
Dolerorthis sp.	2		3	10			1		3			1	2		
Sampo sp.	2	1	3			2	8	4				1		1	
Eospirigerina sp.	2			1	1			8	3	1		6	6		2
Glyptorthis sp.				2				5			4	2	2		2
Orthambonites sp.				4	2		7		1					13	2
Oxoplecia sp.			1	1	1		2	1	2						1
Platystrophia sp.			1	2			1	1				2	1	14	1
Trilobites															
Tretaspis askerensis	3		3	1			1								
Erratencrinurus (*Celtencrinurus*) *kiaeri*			1				1			4		8	1		
Others															
thick stick '*Hallopora*'				7	1		9	6	2	3	5	10	6	6	3
hemisphaeroidal trepostome	10	2		4	1	1		1	1		9	1	2	–0	
streptelasmatid corals	4			2		1	1	4	1	4			1		
Palaeoporella sp.												*	*		*
Total number of specimens	68	13	108	97	8	13	95	90	53	57	71	68	54	116	78
Diversity	17	7	21	28	7	10	29	34	21	16	16	32	22	26	27

Associated fauna includes:

Brachiopods: *Cliftonia* aff. *psittacina* (3), *Christiania* sp. (2), *Coolinia dalmani*, *Dicoelosia* sp. (2), *Diambonia* sp. (2), *Dinorthis* sp.? (2), *Drabovia* sp. (2), *Eochonetes* (2), *Eodinobolus* sp., *Eostropheodonta* sp. (2), *Epitomyonia* sp. (5), *Furcitella* sp. (2), *Gunnarella* sp., *Hesperorthis* sp., *Hindella cassidea* (4), *Hirnantia* sp., *Katastrophomena* sp. (2), *Kjaerina*? sp., *Kjerulfina*? sp. (2), *Kiaeromena*? sp. (2), *Kullervo*? sp., *Laticrura* sp. (2), *Leangella* sp. (5), *Mendacella* sp., *Oepikina* sp. (2), *Paucicrura* sp. (3), *Philhedra* sp. (2), *Plectothyrella*? sp. (2), *Parastrophina*? sp. (2), porambonitacean?, *Rostricellula* sp., *Stegerhynchus* sp. (2), *Skenidioides* sp. (5), *Strophomena* s.s. sp., Strophomenid indet., *Vellamo* sp.

Trilobites: *Acidaspis* cf. *asteroidea*, *Ascetopeltis bockelie*, *Astroproetus*? sp., *Brachyaspis* cf. *robustus*, calymenid (3), *Hadromeros* aff. *keisleyensis*, illaenid indet., *Lonchodomas* sp., *Panderia* sp., proetid indet., *Sphaerexochus* aff. *bridgei*, *Stenopareia* sp., *Toxochasmops* sp. (3).

Molluscs: bellerophontaceans, *Brachytomaria*? sp., *Cymbularia pachygaster*, *Globonema*? sp., *Helicelasma*? sp., *Holopea* sp., loxonemataceans, *Cuneamya*? sp., *Antiplectoceras*? *askerensis*, *Beloitoceras* sp., orthocones indet, *Spyroceras* cf. sp., A (Strand, 1933).

Bryozoans: *Corynotrypa schucherti* (3), *Callopora*? sp., encrusting cyclostome, flat stick trepostome.

Corals: halysitids (4), heliolitids (3), and favositids (3).

Others: *Opikella*? sp. (2), ostracodes indet. (2), *Serpulites* sp. (3), *Tentaculites* sp. (2), *Receptaculites* sp.

Crinoid ossicles are sporadically common, particularly in thin bioclastic beds.

Trace fossils include the ubiquitous *Chondrites* sp.

Average no. of specimens per locality: 64·0.

Mean diversity: 19·3.

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* *Palaeoporella* is common and *in situ* at these localities.

Amongst the thirteen trilobite genera, *Tretaspis askerensis* (Pl. 86, fig. 3) is found in small numbers at localities near the base of the Langåra Formation and *Erratencrinurus* (*Celtencrinurus*) *kiaeri* (Pl. 86, fig. 4) is found higher in the sequence; otherwise trilobites are generally rather rare.

Of the remainder of the fauna, compound corals, including halysitids, favositids, and heliolitids, are particularly obvious at some localities, especially those in Asker, but generally do not constitute a large number of individuals: we have also recorded the alga *Receptaculites* from two localities. Gastropods and bivalves are found in some assemblages, but in small numbers.

The most striking difference amongst the fossil assemblages is the presence or absence of the calcareous alga *Palaeoporella*. This forms dense clusters of calcareous tubes and locally must have formed an algal thicket on the sea floor. It is common in parts of the sequence in Asker from about 20 to 50 m in Stage 5 (Brenchley and Newall 1975), and is clearly *in situ* at some stratigraphical levels. To the south and east it is virtually absent and has been found only as rare fragments in the area around Langåra. Where *Palaeoporella* is well developed it is commonly found enclosed within large nodules. Collecting is generally more difficult at these levels, but brachiopods and other shells appear to be less abundant where *Palaeoporella* is dominant.

The diversity of the *Onniella* Association is high. We have recorded a diversity of thirty-four taxa from a collected assemblage and the average diversity from fifteen assemblages was 19·3, with a mean sample of sixty-four individuals. Although colonization of the sea floor can never have been dense, the presence of brachiopods, bryozoans, corals, and crinoids indicates a varied filter-feeding population. The deposit-feeding elements of the fauna, notably the trilobites and gastropods, are relatively reduced in numbers.

The sediments of the Langåra Formation are very similar to those of the Husbergøya Formation in that they are predominantly mudstones with interbedded sheet sandstones. The texture of the original substrate and the hydrodynamic conditions were apparently similar. The only significant difference is the abundance of diagenetic carbonate, which has formed the courses of nodular limestones in the Langåra Formation. The brachiopods in the assemblages are mainly disarticulated and the trilobites fragmentary, as in the *Tretaspis* Association. However, tabulate corals and *Palaeoporella* are commonly in growth positions.

The increased amount of carbonate in the succession, the greater percentage of sandstone, and the general palaeogeographical reconstruction (Størmer 1967; Brenchley and Newall 1980) all suggest that the *Onniella* Association occurred in a shelf environment, but shorewards and up the palaeoslope from the *Tretaspis* Association.

The Hirnantia *Association* (Table 3)

The *Hirnantia* Association *sensu stricto* is restricted to a few metres at the base of the Langøyene Sandstone (i.e. lowermost Hirnantian) and to one locality at the very top of the Husbergøya Shale and is confined to the eastern part of the Oslo–Asker area. The association is relatively rich in numbers of brachiopods and bryozoans and is moderately diverse. The characteristic brachiopods are *H. sagittifera* and *Dalmanella testudinaria*, which are always accompanied by the encrusting bryozoan *Ceramopora* (Pl. 86, fig. 6) and are usually associated with a thick stick bryozoan resembling *Hallopora*. *Cliftonia* aff. *psittacina* and *Eostropheodonta hirnantensis*, typical brachiopods of the *Hirnantia* fauna elsewhere, occur frequently here in this association but often in small numbers. The trilobite *Mucronaspis mucronata kiaeri* (Pl. 86, fig. 2) is to be found in very small numbers at most localities.

Twelve genera of brachiopods are recorded from assemblages belonging to the association, and five genera of trilobites. Bryozoans are common but appear to be restricted to a few genera. Amongst the rest of the fauna, *Tentaculites* sp., serpulids, and *Cornulites* sp. are quite commonly present, but corals and molluscs are rare. The association has an average diversity of 14·3 from an average sample size of 97·5 individuals.

The *Hirnantia* Association occurs in a unit a few metres thick consisting of interbedded shales and limestones with some sheet sandstones at the base of the Langøyene Sandstone. Not only is this horizon easily recognized lithologically but the large *Hirnantia* valves, commonly encrusted with bryozoa, make this a distinctive faunal horizon. The brachiopod fauna is partly disarticulated but contains about 50% of articulated valves, and appears to be a disturbed neighbourhood assemblage like those discussed previously. The enclosing sediment is mudstone or impure limestone, and appears to be little different in composition from the other shelf mudstones described earlier. The limestone beds consist of clay minerals and calcite in the form of microspar, and could be diagenetic in origin, but their lateral persistence suggests there might be an original carbonate mud component.

TABLE 3. The *Hirnantia* Association

	Localities			
	1	107	18	109
Brachiopods				
Dalmanella testudinaria	27	12	1	8
Hirnantia sagittifera	17	30	5	23
Cliftonia aff. *psittacina*	1	42		1
Hindella cassidea	2	1	1	
Eostropheodonta hirnantensis		5	2	8
Trilobites				
Mucronaspis mucronata kjaeri	4	3	1	1
Bryozoans				
hemisphaeroidal encrusting	7	40	1	17
thick stick '*Hallopora*' sp.	1	31		13
Others				
Tentaculites sp.	1	1	1	1
Cornulites sp.		11		3
Total number of specimens	73	217	16	84
Diversity	15	20	10	12

Associated fauna includes:

Brachiopods: *Acanthocrania* sp., *Glyptorthis*? sp., *Lingula* sp. (2), *Leptaena* sp., *Orbiculoidea* sp., *Oxoplecia* sp., *Philhedra* sp.

Trilobites: *Calyptaulax* sp., *Illaenus* sp., *Platycoryphe* sp., *Toxochasmops* sp.

Others: *Globonema* sp., gastropods indet., bivalves indet, thin stick bryozoa, halysitids, *Serpulites* sp. (2), crinoids roots (2), *Barrandeocarpus* sp.

Average number of specimens per locality: 97·5.
Mean diversity: 14·3.

EXPLANATION OF PLATE 85

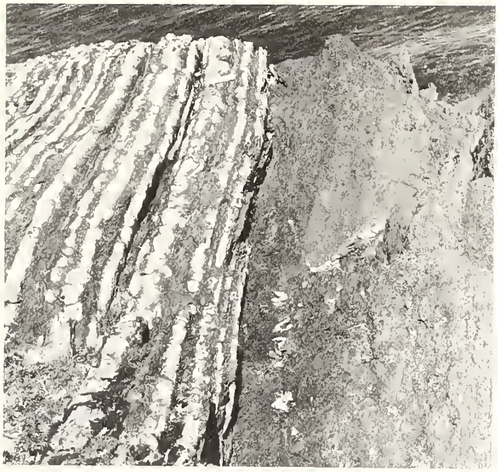
Fig. 1. Boundary between underlying Stage 4*d* γ beds (nodular limestone to left) and grey basal Husbergoya Shale Formation (to right); shore exposure at south-east Rambergøya, Oslo, Grid Ref. NM 965396.

Fig. 2. Sequence of vertical beds younging to the right; shore exposure at south-east Langoyene, Oslo, Grid Ref. NM 966384. Late Ashgill sandstones of the Langøyene Formation are overlain (from hammer head) by a 1 m transgressive sandstone and overlying nodular limestone with an *Onniella* Association, in turn overlain by the dark mudstones without shelly fauna of the basal Llandovery Solvik Formation.

Figs. 3, 4. The beaded trace fossil *Scalarituba*?, possibly representing infaunal feeding traces of a soft-bodied animal; different bedding planes near the top of the Langøyene Formation, south-east Langoyene.

Fig. 5. The large spreite-bearing trace fossil *Trichophycus*?, showing the curved trace to the base of the burrows. This form occurs very commonly at levels about 3 m above the base of the Husbergøya Shale Formation; this example from Skjaerholmen, Grid Ref. NM 966370.

Fig. 6. Conglomerate including rugose corals (e.g. top right) as clastic particles and bored by *Tripanites* holes; 3–4 m from top of Langøyene Formation at south-east Langoyene.



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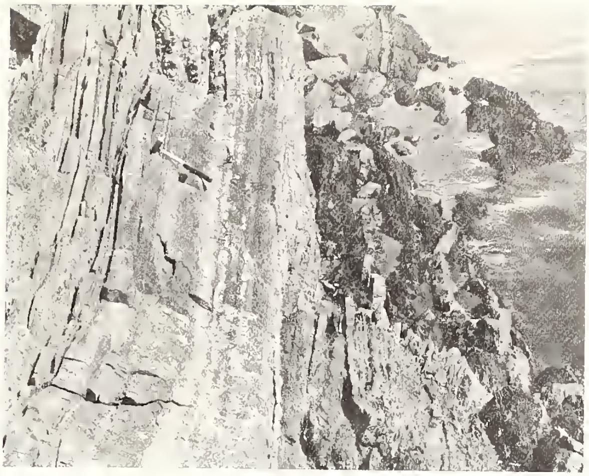

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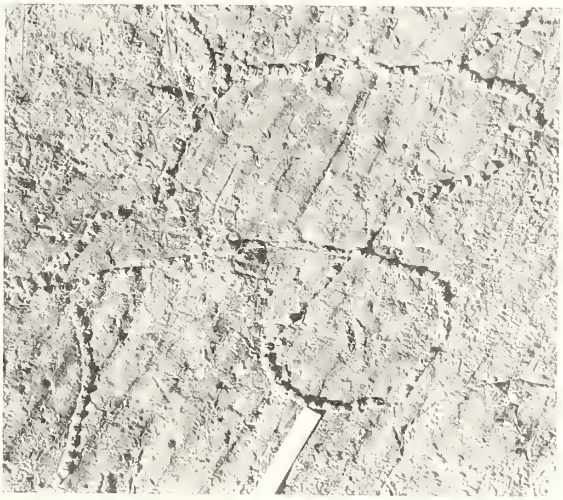

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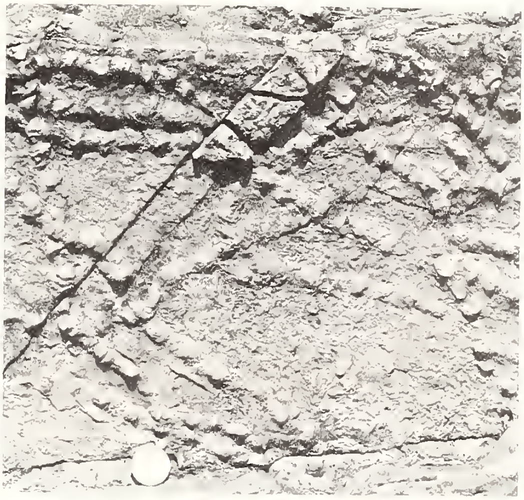

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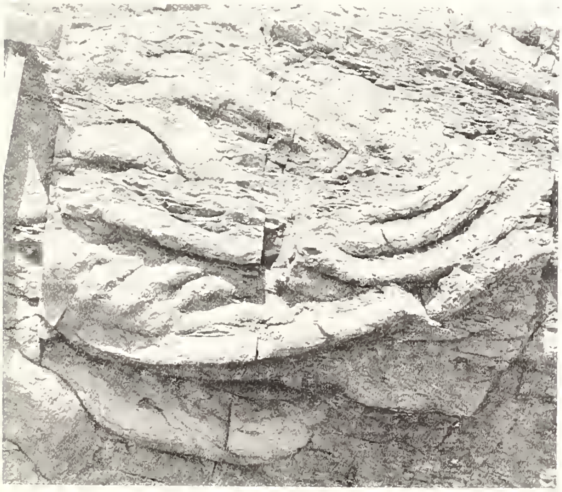

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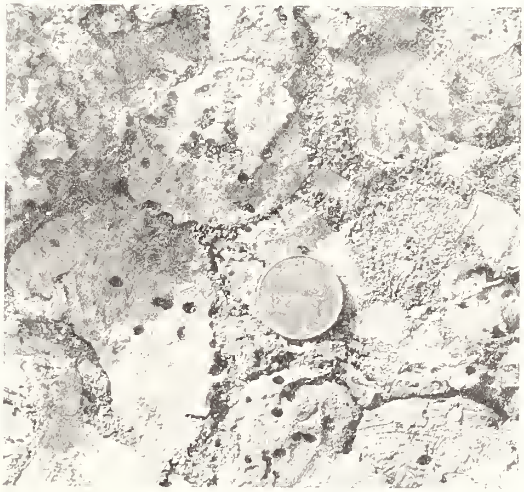

6

BRENCHLEY and COCKS, latest Ordovician of Oslo

This more calcareous horizon apparently represents a continuation of the regression which commenced in the late Rawtheyan and heralds the growth of the shoreface sequence a little higher in the succession. At this stage in the regressive development an inner shelf environment appears to be present (Brenchley and Newall 1980). The relationship of the *Hirnantia* Association with others is discussed in the next section.

The Hindella–Cliftonia *Association* (Table 4)

This association occurs through a few metres of sediment at the same stratigraphic level as the *Hirnantia* Association but is best developed in the western part of the area. The association is characterized by *Hindella cassidea*, *Cliftonia* aff. *psittacina*, and *Dalmanella testudinaria* with *Triplesia* sp. and *Eostropheodonta hirnantensis* as common associates. Thick stick bryozoa (?*Hallopora*) encrusting trepostomes and the streptelasmatid coral *Helicelasma* are also characteristic. The association is closely related to the *Hirnantia* Association s.s. but differs in lacking *Hirnantia* itself and being far richer in *Hindella* and *Cliftonia*.

TABLE 4. The *Hindella–Cliftonia* Association

	Localities								
	33	9	91	30	55	56	74	86	42
Brachiopods									
Hindella cassidea	24	30	4	22	3		1	3	6
Cliftonia aff. *psittacina*	18	110	1	22	5	14	14	5	
Dalmanella testudinaria	11	14	5	3	1	1	1		
Eostropheodonta hirnantensis	4	6	1	2		2			
Triplesia sp.	1		6	6					
Bryozoans									
Hallopora sp.	6	6		11	1				
Corals									
Helicelasma cf. *simplex*	8	50+		8					
Total number of specimens	133	259	20	100	11	19	17	8	6
Diversity	40	23	8	18	5	5	4	2	1

Associated fauna includes:

Brachiopods: *Coolinia dalmani*, *Dolerorthis* sp., *Drabovia* sp., *Eoplectodonta oscitanda* (2), *Eospirigerina* sp., *Eostropheodonta hirnantensis*, *Epitomyonia* sp., *Katastrophomena* sp., *Kullervo*? sp., *Lingula* sp., *Leptaena* sp. (13), *Nicolella* sp., *Onniella kalvoya*, *Orbiculoidea*? sp., orthid indet., *Parastrophina* sp., pentamerid indet., *Platystrophia* sp., porambonitacean indet., rhynchonellid indet., *Sampo* sp., *Skenidioides* sp., strophomenid indet., *Triplesia* sp., *Zygospira* sp.

Trilobites: *Dicranopeltis* aff. *polytoma*, *Harpidella* (s.l.) *occidentalis* (2), *Mucronaspis mucronata kiaeri* (2), *Panderia* sp., *Stenopareia* sp. (2), *Toxochasmops* sp.

Molluscs: bellerophontaceans (2), *Globonema* sp., *Holopella* sp (2), Loxonematacea, platyceratid, *Pleurotomaria*? sp., *Ambonychia* sp., *Cuneamya*? sp., *Beloitoceras* cf. *heterocurvatum*.

Bryozoans: *Hallopora*? sp., hemisphaeroidal trepostome (4), phylloporinid cryptostome, *Rhabdonesonida* sp. (2), thin stick trepostome (2).

Corals: *Grewinkia*? sp., *Leolasma* sp., *Streptelasma* sp. (2).

Others: *Tentaculites* sp. (2), *Receptaculites* sp. (2).

Crinoid ossicles are sporadically common, particularly in thin bioclastic beds.
Trace fossils include the ubiquitous *Chondrites* sp.

Average number of specimens per locality: 63·7.
Mean diversity: 11·6.

The total diversity of brachiopods recorded from the assemblages of this association is twenty-eight, though many of these are found in small numbers at only one or two localities. Bryozoans are common and relatively varied, as are streptelasmatid corals. A varied but sparse fauna of trilobites (six genera) and gastropods (five genera) is present. The preservation of the fauna is that of a disturbed neighbourhood assemblage, apart from locality 33, where a bed containing brachiopods in life position was collected. The diversity of fauna is very variable, ranging from forty to two, with an average, from eight localities, of 15·6 from an average number of 63·7 individuals per locality. The predominance of brachiopods, bryozoans, and corals indicates that the preserved part of this fauna was a filter-feeding assemblage. However, deposit-feeding gastropods are present, and trilobites sporadically found.

The enclosing sediment is like that of the *Hirnantia* Association in being predominantly argillaceous, but is even more calcareous and includes one limestone bed which is up to 1 m thick. Sheet sandstones are absent from these sediments. An inner shelf environment appears to be represented, with the more calcareous aspect indicating a nearer-shore, shallower situation than that of the coeval *Hirnantia* Association s.s.

The Dalmanella *Association* (Table 5)

This association is a very much reduced representative of the *Hirnantia* and *Hindella–Cliftonia* associations. It is strongly dominated by *Dalmanella testudinaria*, and all the other brachiopod genera (total ten) occur sporadically and in small numbers. Other faunal elements are not abundant, though thick stick bryozoa (?*Hallopora*) and encrusting trepostomes are sometimes present. Three genera of trilobites, *Tentaculites* sp., and crinoid debris are also recorded. The highest diversity recorded is twelve and the average diversity from seven localities is 4·9.

The *Dalmanella* Association occurs in mudstones immediately above the *Hirnantia* Association in a regressive sequence, so it is reasonable to assume that it occupied a slightly shallower environment

TABLE 5. The *Dalmanella* Association

	Localities							
	24	41	15	53	54	124	39	34
Brachiopods								
Dalmanella testudinaria	28	21	11	35	5	11	8	24
Cliftonia aff. *psittacina*		2			1			3
Hindella cassidea	1			1	1			
Lingula	1	1	1					
Leangella aff. *cyclindrica*		4	1					
Eoplectodonta oscitanda		4	3					
Bryozoans								
Hallopora? sp.	1	3	2					30
hemisphaeroidal trepostome			1		4			21
Total number of specimens	36	41	21	36	12	11	8	81
Diversity	6	12	8	2	5	1	1	7

Associated fauna includes:
Brachiopods: *Eospirigerina* sp., *Hirnantia* sp. (2), *Nicolella* sp., orthid indet. (2).
Trilobites: illaenid indet, *Mucronaspis mucronata kiaeri*, *Toxochasmops*.
Other: gastropod indet. *Tentaculites* sp.
Crinoid ossicles are found in small numbers at a few localities.
Trace fossils include the ubiquitous *Chondrites* sp.

Average number of specimens per locality: 30.
Mean diversity: 5·3.

on the inner shelf. The only reservation to this conclusion is that *Leangella* and *Eoplectodonta*, which are typical of the deeper-water *Onniella* Association, occur at two localities even though they were absent from the preceding *Hirnantia* Association.

Trematis-Bivalve *Assemblages*

Elements of the *Hirnantia* fauna *sensu lato*, notably *Hirnantia* and *Eostropheodonta*, together with *Plectothyrella* and *Hindella*, are found at a few localities (e.g. 37, 18, 38) in the more sandy sequence overlying the beds with the *Hirnantia* association s.s. At localities 37 and 38 these elements occur rarely and are associated with many specimens of an unusually large inarticulate brachiopod, *Trematis norvegica*, and an abundant bivalve fauna chiefly consisting of modiolopsids, but also including at locality 38 '*Pterinea*' and ?*Cuneamya*. Streptelasmatid corals are also found at this level. These *Trematis*-Bivalve faunas appear to occur at the level where the inner shelf mudstone facies passes into the predominantly sandy facies of the lower shoreface. The actual fauna collected from locality 37, at north Hovedøya, was 32 pedicle valves and 26 brachial valves of *T. norvegica*; 35 specimens, all articulated with both valves and apparently in life position, of the modiolopsid bivalve; 10 large conulariids; 3 articulated *Hindella cassidea* and one disarticulated pedicle valve; one articulated specimen each of *Hirnantia*, *Eostropheodonta*, and *Leptaena*; and a further disarticulated brachial valve of *Eostropheodonta*; a total of 85 specimens with a diversity of 7.

The Holorhynchus *Association* (Table 6)

This association is found only in the north-west part of the study area, where it occurs above beds with an *Onniella* Association, near the top of the Langåra Limestone-Shale Formation. Through about 8 m of section *Holorhynchus giganteus* dominates the fauna, being generally dispersed through the silty mudstones but sometimes being sufficiently densely packed to form shell banks. We have made three collections from near Sandvika (section 29) which, together with field observations from locality 26 at Holmen, show the fauna to be fairly homogeneous. *H. giganteus* is nearly always the dominant form in the association, but *Eoplectodonta rhombica* is well represented and *Onniella* sp. and *Leptaena* sp. are usually present. Thick stick bryozoans are usually quite common, and both streptelasmatid and tabulate corals are normally present. Thirteen genera of brachiopods are recorded from the assemblages in the association, which is a marked reduction from the underlying

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EXPLANATION OF PLATE 86

Fig. 1. *Tretaspis sortita* (Reed) *broeggeri* Størmer, latex cast of a cranidium × 3, PMO 103963 from uppermost Husbergøya Formation at Hovedøya.

Fig. 2. *Mucronaspis mucronata* (Brongniart) *kiaeri* (Troedsson), cranidium × 4, PMO 101549, from 1·6 m. below the top of the Husbergøya Formation at south-west Rambergøya, Grid Ref. NM 961394.

Fig. 3. *Tretaspis askerensis* Owen, cranidium ×6, PMO 100657, from near the base of the Langåra Limestone-Shale Formation, Holmenskjaerest, Asker, Grid Ref. NM 838363.

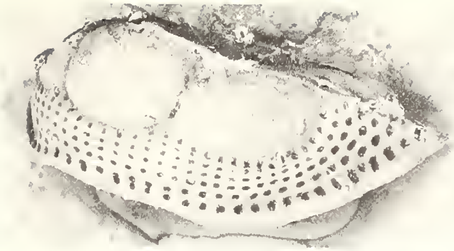
Fig. 4. *Erratencrinurus* (*Celtencrinurus*) *kiaeri* Owen, cranidium × 2·5, PMO 11291, from Langåra Limestone-Shale Formation, Nybårg, Asker.

Fig. 5. *Stygina latifrons* (Portlock) *extensa* (Reed), cranidium and thorax moult in Salter's position, ×2·5, PMO 97018, from whithin 1 m below the top of the Husbergøya Formation, Husbergøya, Grid Ref. NM 961375.

Fig. 6. The cystoporate bryozoan *Ceramopora* encrusting a *Hirnantia* shell, BB 93948, latex cast ×2, from top 15 cm of Husbergøya Formation, Rambergøya west, Grid Ref. NM 962394.

Fig. 7. The meandering trace fossil *Helminthopsis* from the Langøyene Formation, north Hovedøya, Oslo, Grid Ref. NM 967416.

Fig. 8. Burrows of *Monocraterion* in parallel laminated sandstones of the lower shoreface, Langøyene Formation, west Rambergøya, Grid Ref. NM 960394.



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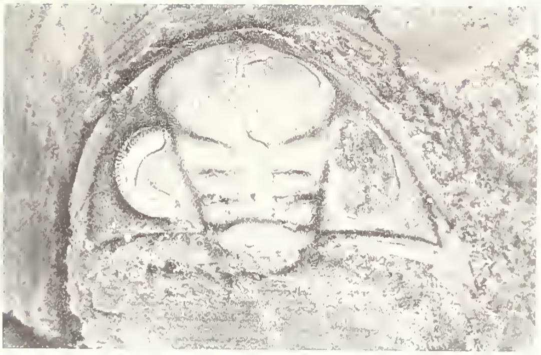

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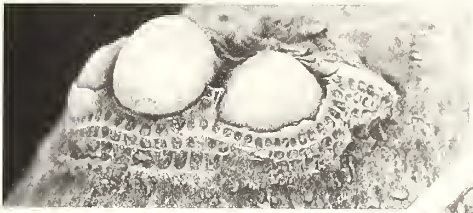

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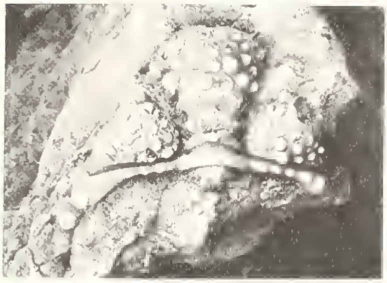

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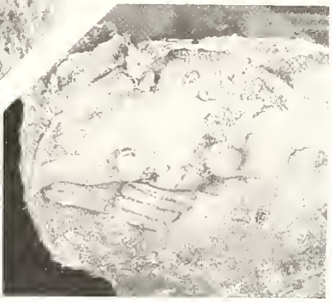

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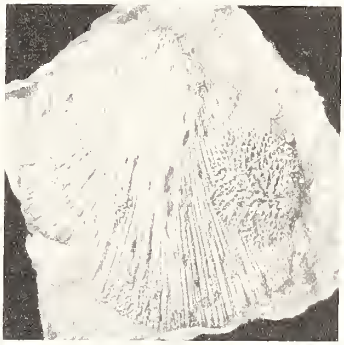

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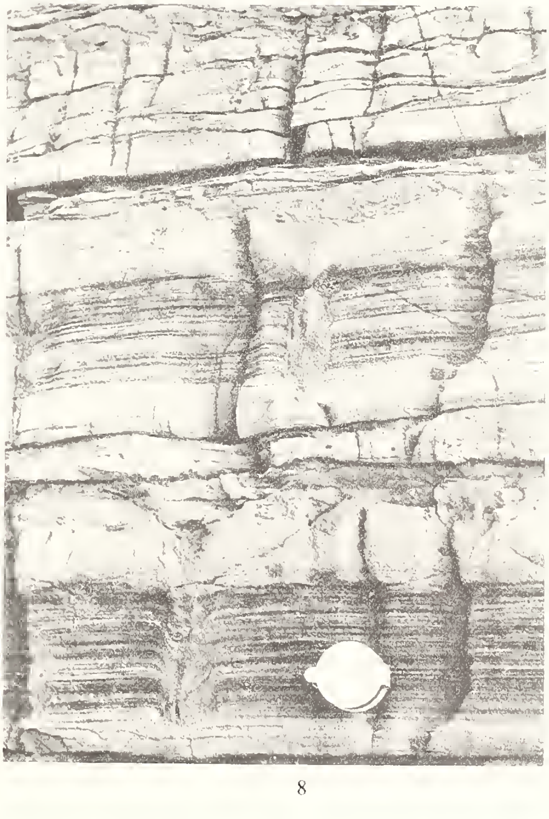

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BRENCHLEY and COCKS, latest Ordovician of Oslo

TABLE 6. The *Holorhynchus* Association

	Localities		
	5	106	44
Brachiopods			
Holorhynchus giganteus	31	95	15
Eoplectodonta rhombica	15	10	13
Onniella sp.	4	10	1
Leptaena sp.	2	2	2
Dolerorthis sp.	4	3	
Nicolella sp.	1		3
Bryozoans			
Hallopora? sp.	2	15	2
Corals			
streptelasmatid	2	24	
halysitid	2	3	
heliolitid		3	1
favositid		10	3
Bivalves			
modiolopsid indet.	1		
Total number of specimens	84	205	38
Diversity	17	21	8

Associated fauna includes:

Brachiopods: *Eospirigerina* sp., *Hesperorthis* sp., *Katastrophomena* sp., *Leangella* aff. *cylindrica*, *Paucicrura* orthid indet., pentamerid indet., *Sericoidea*? sp.

Molluscs: gastropods indet., pleurotomariacean, nuculid? bivalve, *Similodonta*? sp., *Discoceras*? sp. indet.

Bryozoans: Hemisphaeroidal trepostome, thin stick trepostome, encrusting net bryozoan.

Other: *Receptaculites* sp.

Crinoid ossicles are rare.

Trace fossils include the ubiquitous *Chondrites* sp.

Average number of specimens per locality: 109.

Mean diversity: 15·3.

Onniella Association. The sediment in which the *Holorhynchus* Association is found is less calcareous than that lower in the sequence but is more silty, and this probably reflects the shallower situation of the *Holorhynchus* Association.

The Thebesia *Association* (*Channel-fill faunas*) (Table 7)

This association is mainly dominated by the rhynchonellid *Thebesia scopulosa*, often with *Hindella*, *Comatopoma*, and *Leptoskelidion loci*, and occurs in the upper horizons of the tidal channel at Hovedoya (section 10), and in a more restricted form at the top of sandstones filling a channel at Langoyene locality 125, section 5. Corals are associated with the brachiopods in some beds, with *Palaeophyllum* being particularly abundant at Hovedøya, and streptelasmatid corals and bryozoa being sporadically present and common on some bedding planes.

Those tidal channels which were cut through the shoreface sandstones in the south of the area, or through mudstones in the north-west of the area, tend to be wide and filled with a varied suite of allochthonous sediments. In contrast, the channels which were cut through lithified oolitic limestone

TABLE 7. The *Thebesia* Association and other Channel-fill Faunas

	Localities					
	76	77	16	78	14	125
Brachiopods						
Thebesia scopulosa	97	14		65	15	
Hindella cassidea	26	25		17	4	
Comatopoma sp.	3	1	1	12		4
Leptoskelidion loci	24	7		8	3	
Corals						
Palaeophyllum sp.				20+		
streptelasmatid corals		2		7		
Bryozoans						
thin stick trepostome				5		
thick stick trepostome	2		3			5
hemisphaeroidal trepostome			18			
Total number of specimens	169	52	36	151+	23	11
Diversity	9	6	8	19	4	4

Associated fauna includes:
Brachiopods: *Dalmanella* sp., *Dolerorthis*? sp., *Eostropheodonta* sp., *Hesperorthis*? sp., *Kjaerina*? sp., *Onniella* sp., orthid indet., *Philhedra* sp., *Stegerhynchus*? sp., strophomenid indet.
Trilobite: *Mucronaspis* sp.
Molluscs: *Holopella*? sp., pleurotomariacean, orthocones indet.
Corals: *Sarcinula* sp., favositid
Other: cornulitid.
Crinoid ossicles are sporadically common amongst the bioclastic debris.
Trace fossils include *Chondrites* sp. and varieties of *Planolites* spp.

Average number of specimens per sample: 73·7.
Mean diversity: 8·1.

in the central belt shown in text-fig. 7 (Brenchley and Newall 1980) were narrow and were filled with a sequence of different sediments. The Hovedøya Channel is lined with fallen blocks of oolitic limestone covered by sandstone, and this shows evidence of high current-velocities. The channel was finally filled by bioclastic sediments with brachiopod coquinas and coral-rich beds. The brachiopods in the coquinas have a mixture of articulated and disarticulated specimens and the corals occur as substantial colonies. The faunas appear to be disturbed, though essentially *in situ*, assemblages, and they lived within channels which had been first partly filled and then become relatively inactive, allowing local colonization of the sea floor. This is well illustrated at locality 125 (section 5, Langøyene), where conglomerates which infill a broad channel have a surface at the top where the limestone clasts are bored by *Tripanites* sp. (Pl. 85, fig. 6), suggesting a stabilization of the pebble fill. Overlying the conglomerates are sandstones with *Comatopoma* sp. and bryozoans.

The Brevilamnulella *Association* (*Coquina fauna*) (Table 8)

At two general localities very near the top of the Ordovician, one in the central belt and the other in the north-west part of the study area, there are coquinas dominated by the pentameracean *Brevilamnulella kjerulfi*. Throughout most of the central belt the uppermost Ordovician is represented by oolitic limestones (text-fig. 8) which contain few fossils, and none that are untransported. However, at Hvalsbakken (section 20, text-fig. 1) there is a development of up to 9 m of bioclastic limestone containing some ooids, which might either be a local facies variant of the ooidal shoals or alternatively might lie within a channel cut into the oolite. These bioclastic limestones contain abundant *Brevilamnulella*, together with a small number of other brachiopods, and rare tabulate and rugose corals and bryozoans in some beds. The valves of *Brevilamnulella* are predominantly disarticulated but unbroken, and because of the dense and virtually monospecific accumulation of shells it seems likely that the assemblages, though transported, are of local origin.

The second occurrence of the *Brevilamnulella* fauna is found at the northern margin of the study area at two places near Sem Vatern (Grid Refs. NM 799364, NM 800364,) where it is abundant in several beds in calcareous siltstones near the top of the Ordovician sequence at each locality.

The *Brevilamnulella* Association has a low diversity and in terms of brachiopods is nearly monospecific in some beds. However, at Hvalsbakken some bedding planes have yielded *Brevilamnulella* in association with two species of corals and two types of bryozoans. The association appears to represent a localized but successful colonization of the very late Ordovician sea floor.

TABLE 8. The *Brevilamnulella* Association (Coquina Fauna)

	Localities					
	80	11	81	82	69	70
Brachiopods						
Brevilamnulella kjerulfi	37	70	8	14	25	72
Rostricellula? sp.		3	1			
Bryozans						
Hallopora sp.	4	3	2			
Corals						
Streptelasmatid	4		1	2		
Total number of specimens	46	78	14	26	28	73
Diversity	4	3	6	8	2	2

Associated fauna includes:

Brachiopods: *Eoplectodonta oscitanda*, *Eospirigerina* sp., *Hesperorthis*? sp., *Hindella* sp. (2), *Leptaena* sp., *Onniella* sp.

Others: pleurotomariacean, single rugose corals indet., heliolitid, *Palaeoporella* sp.

Crinoidal ossicles occur in some of the bioclastic beds.

Average number of specimens per sample: 44·2.
Mean diversity: 4·2.

The Monocraterion *Association*

The Langøyene Sandstone Formation yields very few body fossils except from localities near the base and a few localities in the transgressive facies at the top. However, trace fossils are intermittently common through the sandstone sequence, and are particularly common in the lower part where the sandstones are thinly bedded. *Monocraterion* sp. (Pl. 86, fig. 8) is common at several horizons in the eastern part of the study area, and *Planolites* and *Chondrites* occur where there are thin mudstone partings between sandstone beds. Traces, probably referable to *Helminthopsis* sp. (Pl. 86, fig. 7) also occur on some bedding planes. Coarse sandstones and conglomerates filling tidal channels form a major part of the middle and upper part of the formation, and these sediments generally have no ichnofauna. However, sandstones overlie channels in some places near the top of the succession and these contain a very distinctive, large, beaded, infaunal trace (Pl. 85, figs. 3, 4) which was called *Scalarituba* by Seilacher and Meischner (1965, p. 615).

Where the Langøyene Sandstone contains more interbedded shale beds, as at Hovedøya, the trace fossil fauna is particularly varied and includes *Chondrites*, *Planolites*, *Monocraterion*, *Nereites?* sp., *Phycodes*, *Teichichnus*, *Helminthopsis?*, *Diplichnites*, and a trace similar to *Thalassinoides* (see *Monocraterion–Teichichnus* Association on text-fig. 7). Brenchley and Newall (1975) have interpreted this more shaly facies as forming offshore from the more sandy shoreface facies to the south (see text-fig. 8).

Faunas of the Silurian Transgressive Sequence

The Stage 5 sequence ends with a thin transgressive sand sheet, containing a diverse *Onniella* assemblage (Table 9), chiefly including smaller forms; this sheet is present over most of the Oslo district. The sand forms the lower part of a distinctive couplet, of which the upper part is a nodular limestone about 60 cm thick with a sparse fauna of *Eospirigerina* and other brachiopods, illaenid trilobites, and orthocones. To the east of the area, at Hovedøya, Rambergøya, and nearby localities, this couplet is succeeded by dark shales (Pl. 85, fig. 2) with no shelly fauna, although some bedding planes have abundant graptolites. Howe (1982) has reviewed these graptolites and notes the presence of very early Llandovery *acuminatus* Zone forms 11 m above the base of the dark shales at Ormøya, indicating that the time, if any, unrepresented by rock near the Ordovician–Silurian boundary in the area is minimal. To the west of the area there are no dark shales, and the Llandovery transgression did not deepen the water beyond depths colonized by shelly benthos. For example, a locality near Sandvika (Grid Ref. NM 851403) yielded a diverse assemblage of the Llandovery *Clorinda* Community in a continuous section 7 m above the top of the *Holorhynchus* Beds, as did a temporary road section near Holmen (Grid Ref. NM 836363). At another locality, at Konglungen (Grid Ref. NM 850347), a rich assemblage dominated by *Triplesia* was collected in position of growth 2 m above the base of Stage 6. Similar early Silurian faunas are widespread and have been described from Britain (Ziegler, Cocks and Bambach 1968; Cocks and Toghill 1973) from both sides of the Iapetus Ocean.

TABLE 9. The *Onniella* Association in Transgressive Facies

	Localities		
	21	87	94
Brachiopods			
Eoplectodonta oscitanda	16	17	
Leangella aff. *cylindrica*			
Paucicrura sp.	4		13
Onniella kalvoya		17	
Dolerorthis sp.	5	1	
Bryozans			
thin stick trepostome	1	2	2
Hallopora?	13		3
Total number of specimens	103	48	36
Diversity	17	9	13

Associated fauna includes:

Brachiopods: *Cliftonia* aff. *psittacina*, *Dalmanella testudinaria*, *Dicoelosia* sp., *Laticrura* sp., *Leptaena* sp., *Leptoskelidion loci*, *Lingula* sp., orthid indet., *Rostricellula* sp., *Skenidioides* sp., *Stegerhynchus*? sp., *Thebesia scopulosa*.

Trilobites: *Decoroproetus exevus*, *Stenopareia* sp.

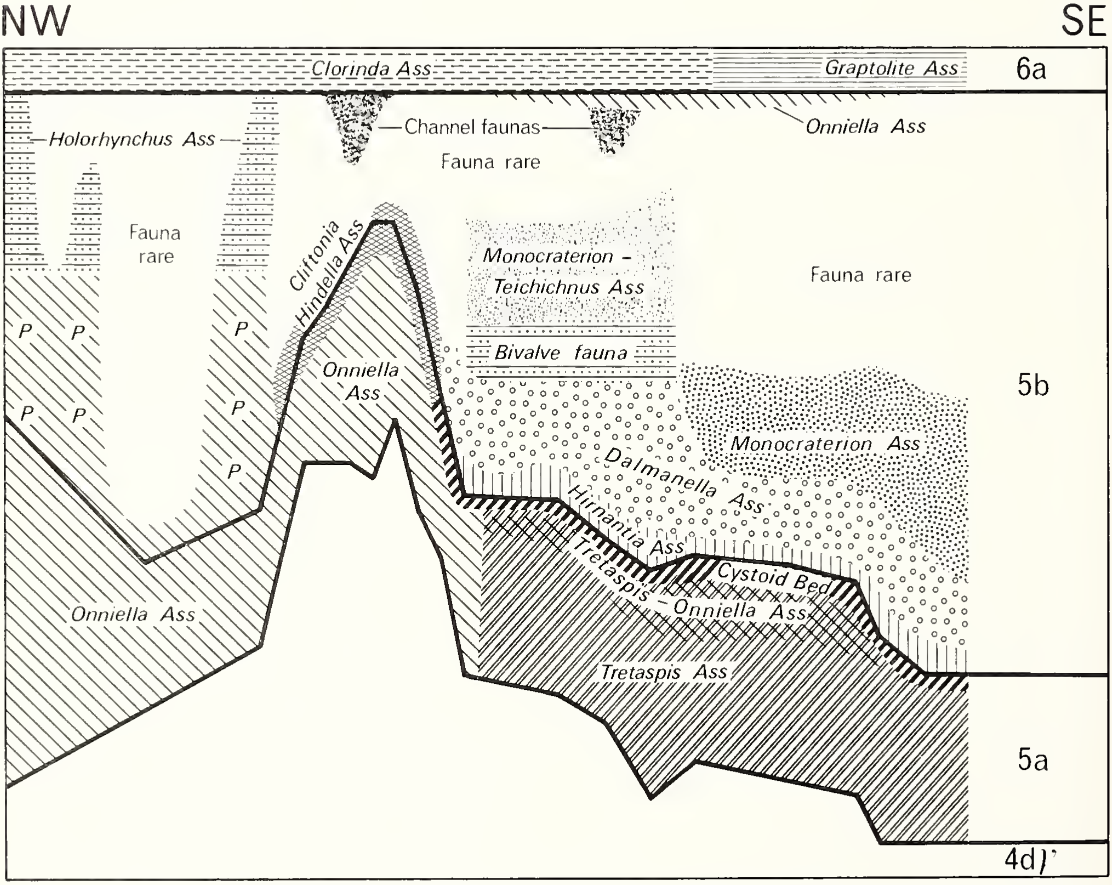
Others: hemisphaeroidal trepostomes (2), orthocones indet.

Crinoid ossicles are common at each of the three localities.

ENVIRONMENTAL DISTRIBUTION OF THE ASSOCIATIONS

The vertical and lateral distributions of the faunal associations are shown on a stratigraphical profile in text-fig. 7. The vertical sequence of faunas reflects the progressively shallower conditions evolving during the latest Ordovician glacio-eustatic regression, whilst the lateral changes reflect the lateral differences in bathymetry throughout the region. A comparison between text-figs. 7 and 8 shows that the faunal associations are closely related to the varied late Ordovician environments, and range from the *Tretaspis* Association in a relatively deep shelf environment to the *Monocraterion* Association developed on the lower and middle shoreface.

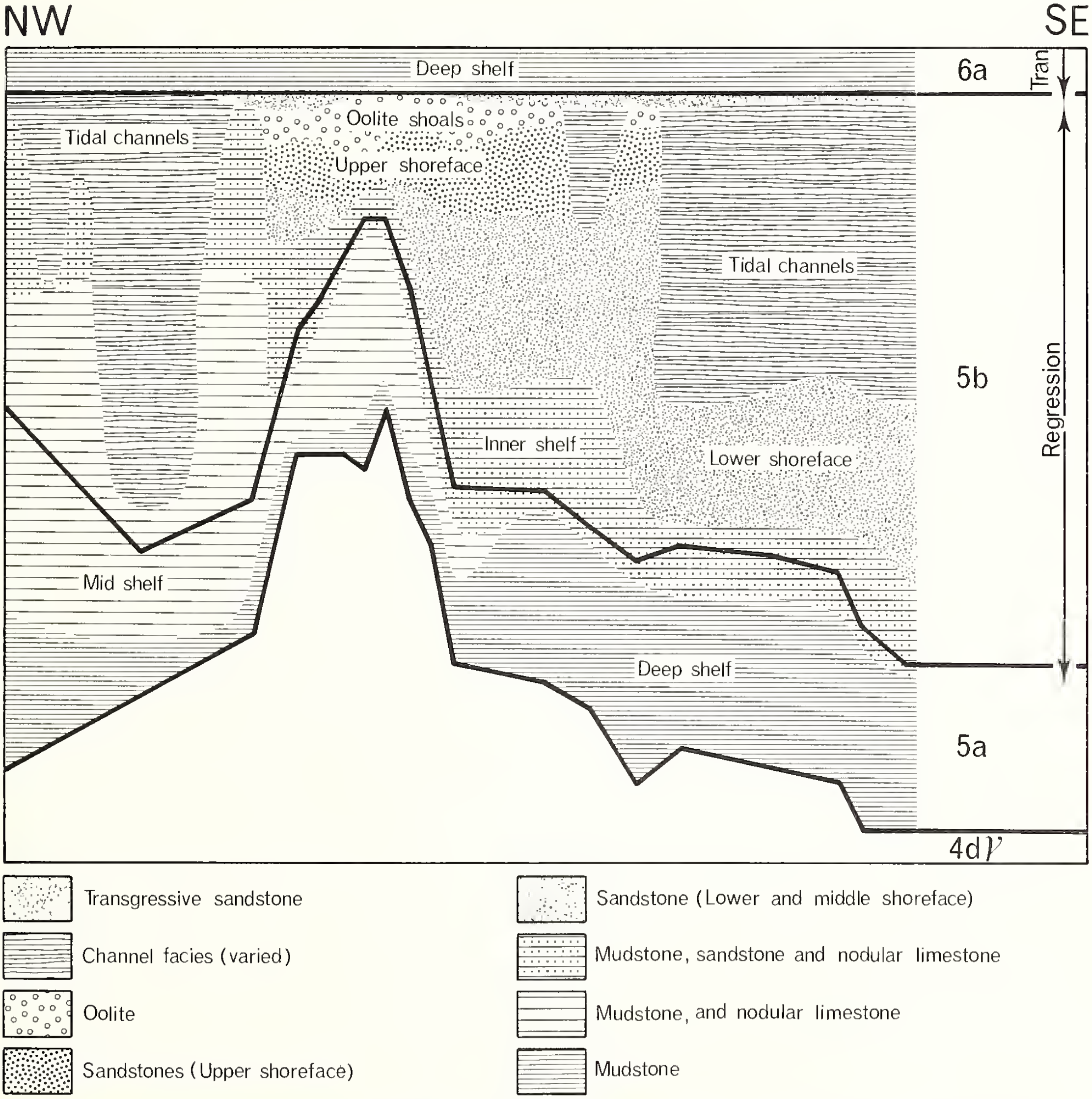
The faunal associations in Stage 5*a* (later Rawtheyan) of the study area were all situated in a shelf environment (text-fig. 9), with the highly diverse *Onniella* Association in the more calcareous muds towards the shore, and the sparser and less diverse *Tretaspis* Association further down the palaeoslope. It is difficult to make an estimate of absolute depth for the associations or to identify their specific location on the Ordovician shelf. The absence of lamination within the silty argillaceous sediments suggests they were not generally affected by bottom currents, but the disarticulation of a substantial proportion of the bivalved specimens suggests that there may have been some stirring of the muddy sediments. We have suggested earlier that this might be the effect of deep waves during



TEXT-FIG. 7. Stratigraphical profile from north-west to south-east across the study area (cf. text-figs. 2 and 3) showing the stratigraphical distribution of the faunal associations.

storms. Since the Oslo–Asker district lay a substantial distance (300 km+) east of the platform margin it is very probable that it was protected from the most severe of the oceanic swells, and storm-wave base would have been at a relatively shallow depth. Bottom sediment stirring can occur to depths of 125 m or more on high-energy coasts, but occurs at considerably shallower depths on low-energy coastal margins (Komar 1979), and therefore a depth less than 100 m might be regarded as likely for the *Tretaspis* Association.

An alternative estimate of maximum depth can be made because the late Ordovician regression apparently exposed the whole area, which is suggested to have involved a sea level change of no more than 100 m (Brenchley and Newall 1980), and so we again regard this as the likely maximum depth for



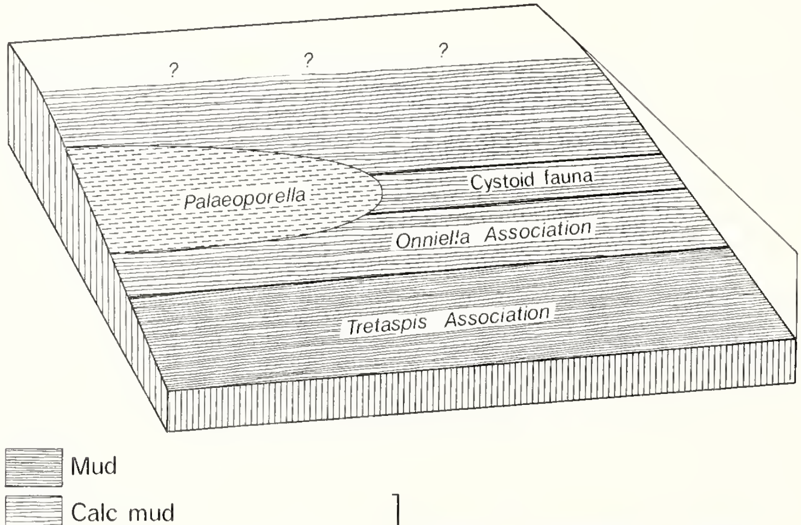
TEXT-FIG. 8. Stratigraphical profile from north-west to south-east across the study area (cf. text-figs. 2, 3, 7) showing the distribution of sedimentary environments.

the *Tretaspis* Association. The transition down the palaeoslope from the *Onniella* Association to the *Tretaspis* Association involves a shift from brachiopod-, bryozoan-, and coral-dominated filter-feeding faunas to trilobite- and gastropod-dominated deposit-feeding faunas, which probably reflects the decrease in food supply with both increase in depth and distance from shore.

The Stage 5*b* (Hirnantian) associations range from mid-shelf to middle-shoreface environments (text-figs. 7 and 10). The *Hirnantia* fauna *sensu lato* lived in a shelf environment, but we are able to subdivide that fauna into a *Hindella–Cliftonia* Association and a nearer-shore *Hirnantia* Association *sensu stricto*. A third, closely related, *Dalmanella* Association possibly lived in an intermediate situation, but this cannot be clearly demonstrated since the three associations do not occur in a single vertical succession. In addition to the rather low-diversity *Dalmanella* Association, there are a few assemblages which are found in the sandy sediments of the lower shoreface and which are dominated by either *Cliftonia* or *Hindella*, with very small numbers of other subsidiary species of macrofauna. We interpret these assemblages as representing some of the shallower benthic assemblages in the clastic facies of the area.

The precise environment position of the *Holorhynchus* Association is difficult to establish because, although it occurs in a shelf environment shallower than the stratigraphically underlying *Onniella* Association, it does not occur in a stratigraphical sequence with the *Hirnantia* fauna. *Holorhynchus* is confined to the north-west of the study area, and its distribution is patchy in a manner resembling the shell banks formed by large pentamerids such as *Pentamerus* and *Kirkidium* in the Silurian. We have tentatively placed the *Holorhynchus* Association at a depth similar to that of the *Hirnantia* faunas in text-fig. 10, but suggest that it may have lived closer to a carbonate shoreline, where food may have been more freely available.

The shallowest of the benthic associations with body fossils found in the clastic facies is the *Trematis*–Bivalve Association, characterized by *Trematis norvegica* and modiolopsid bivalves. This fauna has been found at only two localities, where the transition from shelf to shoreface appears to have been relatively gradual. In such situations the Bivalve association is succeeded stratigraphically by a trace fossil fauna with *Monocraterion*, *Teichichnus*, and other horizontal burrows. Where the shelf-to-shoreface transition was more rapid the *Trematis*–Bivalve Association and *Teichichnus* have



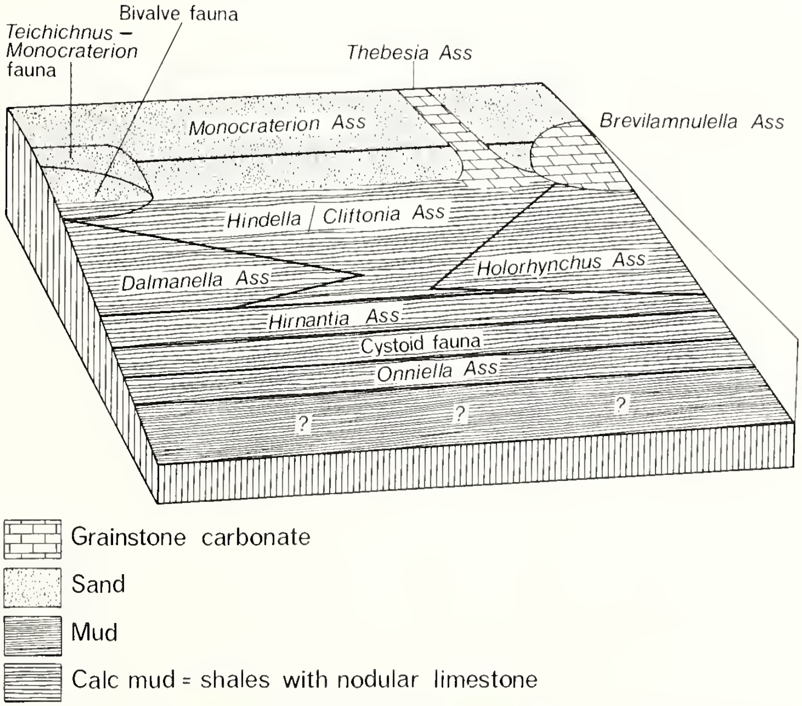
TEXT-FIG. 9. A reconstruction of the distribution of late Rawtheyan faunal associations in the Oslo–Asker area.

not been found (text-fig. 7). The transition from bioturbated muds and silts of the inner shelf to sands of the shoreface is unlikely to have occurred at a depth greater than 20 m (cf. Sanders and Kumar 1975) and was probably considerably less.

The shallowest faunas in the carbonate environment are those of the *Brevilamnulella* Association, which are found intimately associated with ooidal tidal shoals. These faunas lived either in the more stable parts of the shoals which could be colonized, or in shallower channels within the oolites. The *Thebesia* Association is certainly found within tidal channels cut through the oolites, but, judging by the presence of substantial coral colonies, the faunas probably colonized the channels when they were relatively inactive and had been partially drowned during a transgressive episode.

At the very end of the Ordovician the shallower marine clastic and carbonate environements were rapidly inundated during the transgression, reflecting the first phase of the melting of the Gondwanan icecaps (Brenchley and Newall 1980). The *Thebesia* faunas in the tidal channels might have developed during the very earliest phase of this transgression. However, the faunas of the *Onniella* Association are much more widespread, and are found in the thin veneer of bioturbated sand which blanketed much of the Oslo–Asker area. These are first succeeded by sparse faunas including *Eospirigerina*, often in reworked carbonates, and then by faunas of more typically Silurian aspect, such as the *Clorinda* faunas of the west and the graptolites to the east, a distribution which reflects the local re-establishment of the eastward-facing palaeoslope in early Llandovery times.

The distribution of the associations in relation to their environments indicates that they occupied fairly specific parts of the late Ordovician shelf, and to this extent were depth-related. The texture of the substrate can have had little influence on the distribution of the faunas because most of the associations are found in silty mudstones of similar grain size. The chief variation amongst the shelf sediments lies in the amount of carbonate present, which is reflected today in the abundance of



TEXT-FIG. 10. A reconstruction of the distribution of Hirnantian faunal associations in the Oslo–Asker area.

limestone nodules. It is possible that early cementation of the carbonate gave some sediments a greater cohesion, and thus affected the substrate favourably for colonization by an epifauna, but there is no evidence that contemporary cementation proceeded far enough to give rise to hardground surfaces. Where unstable sandy substrates were developed on the shoreface, these were almost wholly devoid of shelly epifauna and were populated only by an infaunal burrowing benthos, represented particularly by the trace fossil *Monocraterion*.

The role of food resources in partitioning the benthos is always difficult to assess; however, the faunas of the study area are found in shales with nodular limestones, and the nodules generally decrease in abundance with distance from shore. The $\delta^{13}C$ values in the nodules are close to zero (J. Gluyas, pers. comm.), which suggests that, although they are of diagenetic origin, they developed from original biogenic carbonate. Biogenic carbonate mud is likely to have been formed either from algae or microplankton, and may therefore represent potentially high food levels available for macrofauna. Conversely, the poor development of carbonate nodules in the sediments containing the *Tretaspis* Association might reflect the lower resource levels available to this deeper-water fauna.

TABLE 10

	Brachiopod diversity			Trilobite diversity			Total diversity
	max	min	average	max	min	average	average
Tretaspis Association	3	0	1·2	7	1	3·7	6·2
Onniella Association	18	4	12·7	5	0	1·5	19·3
Hirnantia Association	9	5	6·5	3	1	2·0	14·3
Hindella–Cliftonia Association	25	1	6·3	5	0	1·2	11·6
Dalmanella Association	8	1	4·0	2	0	0·4	5·3
Holorhynchus Association	9	5	7·7	0	0	0	15·3
Thebesia Association	9	4	5·8	1	0	0·2	7·8
Brevilamnulella Association	7	1	3·2	0	0	0	4·2
Transgressive *Onniella* Association	13	5	8·0	3	0	1·0	13·0

The estimated total diversity, in particular the diversity of the brachiopod fauna (apart from the relative lack of brachiopods in the deepest-water *Tretaspis* Association), varies with depth and distance from shore (Table 10). The nearshore associations, such as the *Brevilamnulella*, *Dalmanella*, and *Trematis–Bivalve* associations, and the *Hindella–Cliftonia* assemblages found in sandy sediments, all have rather low diversities; and mean diversity reaches a peak in the *Onniella* Association. It is the filter-feeding elements of the associations which determine this pattern, because if the deposit-feeders alone are considered, then the maximum diversity is reached in the deeper-shelf *Tretaspis* Association. This pattern of diversity, with low mean values nearshore, a mid-shelf peak, and then declining values with greater depth, is similar to that found in other studies of Lower Palaeozoic faunas (Calef and Hancock 1974; Hurst 1979*a*; Lockley 1980). The increasing values away from shore are best explained by the stability–time hypothesis of Sanders (1969), whilst the drop in density and diversity towards the outer part of the shelf was probably the result of relatively low levels of food supply which apparently affected Lower Palaeozoic communities much more severly than modern ones, perhaps caused by the relatively ill-ventilated state of seas at that time (Leggett *et al.* 1981).

COMPARISON WITH OTHER ASHGILL FAUNAS

Comparison of the Oslo associations with those from other contemporary sequences is hampered by the absence of studies through the faunal succession elsewhere. However, there are many assemblages known from one or two detailed localities in many areas of late Ashgill age, in particular the many descriptions of *Hirnantia* faunas in recent years. These include faunas from Poland (Temple 1965), Bohemia (Marek and Havlíček 1967), Morocco (Havlíček 1971), England and Wales (Temple 1965; Cocks and Price 1975; Hiller 1980), Ireland (Wright 1968), Canada (Lespérance and Sheehan 1976; Cocks and Copper 1981), the United States (Amsden 1974), Kazakhstan (Appollonov, Bandaletov and Nikitin 1980), China (Rong 1979), and South Africa (Cocks *et al.* 1970), and the fauna has also been briefly reported from other areas such as Belgium and Burma. In Scandinavia the *Hirnantia* fauna has previously been recognized in Sweden by Bergström (1968), and Sheehan (1979) has discussed its palaeoecology. By contrast, faunas of Rawtheyan age have not been fully described from an ecological standpoint from anywhere, and their systematics only partially revised, for example the brachiopods from North Wales (Hiller 1980) and the trilobites from Kildare, Ireland (Dean 1970–1978). However, lower Ashgill (Pusgillian and Cautleyan) palaeoecological studies have been made on material from the United States (e.g. Bretsky 1970) and Canada (Copper 1978), but these are in the Richmondian, which does not appear to be directly comparable with the Oslo–Asker region either in the taxa present or in the composition of its ecological associations. The *Orthambonites–Leptestiina* and *Onniella–Skenidioides* Associations reported by Harper (1979) from Girvan, Scotland, appear to include forms which occur in our *Onniella* Association, and it is also relevant to note that Harper is able to divide his Hirnantian faunas from the High Mains Sandstone Formation into two, which he terms *Eostropheodonta–Hindella* and *Hirnantia–Hindella* Associations.

The Oslo–Asker faunas are also quite different from those found in the carbonate mounds of Rawtheyan age (and thus contemporary with the lower part of our study area) which are developed in several places in the Anglo-Baltic area, particularly in Kildare, Ireland; Keisley, northern England; and Boda, Sweden. Other bioherms, such as that at Portrane, Ireland, are of earlier ages in the Ashgill. Smaller reefs are also known from near Oslo, for example the one of probable Rawtheyan age at Ullerntangen, Ringerike, but, despite the variety of ecological niches available in such bioherms and the large and diverse number of species which occur in them, there are very few species in common between these habitats and those of the more open shelf and shoreface deposits of the Oslo–Asker area.

The variable shallow-water deposits and faunas from our area are seldom preserved in rocks of late Ashgill age. In particular, the *Monocraterion* Association and the Channel-fill (*Thebesia* Association) and coquina (*Brevilamnulella* Association) faunas are preserved nowhere else, except on the North American craton (Amsden 1974), and it is a surprise to find such apparently specialized and widely dispersed faunas with such close similarities in composition and taxa. However, faunas dominated by *Holorhynchus* are known from several areas, notably in the Ulkuntas Beds of Kazakhstan (Sapelnikov and Rukavishnikova 1975), where the associated fauna, especially of corals and brachiopods, appears to be much more diverse than in Oslo–Asker. As in Oslo–Asker, the precise stratigraphical relationships of the *Holorhynchus*-bearing beds and those with the *Hirnantia* faunas are difficult to establish, and their detailed age (although undoubtedly late Ashgill) and ecological position appear uncertain. *Holorhynchus* has also been identified in the late Ashgill Porkuni Beds of Estonia.

Although the identification and correlation of mid-shelf and shallower-water faunas of Hirnantian age is now well established, problems still remain in the recognition of deeper-water faunas. Now that the *persculptus* Zone is known to represent at least the later part of the Hirnantian, it is possible to identify some deeper-water faunas as being Hirnantian in age. These include the shells and trilobites known from the so-called *Atrypa flexuosa* Limestone at the base of the Skelgill Beds in the Lake District of northern England (Marr and Nicholson 1888). That Limestone yields forms which can be reidentified as including *Kinnella*, *Ravozetina*, *Paromalomena*, and other genera which, although occurring with *Hirnantia* faunas elsewhere, are absent from the Oslo–Asker area. This suggests that the *Hirnantia* fauna *sensu lato* (i.e. the *Hirnantia* community of Cocks and Price 1975 occurred in a fairly wide range of depths on the shelf. Our work in the Oslo Region and that by Harper (1979) near Girvan, Scotland, shows that the *Hirnantia* fauna was partitioned into fairly discrete associations which probably reflect several environmentally controlled communities. Some genera, notably *Hirnantia*, *Eostropheodonta*, *Plectothyrella*, and possibly *Dalmanella*, although exhibiting an environmental preference for an inner shelf environment, were eurytopic and apparently thrived over a wider depth range than was usual for other brachiopod genera in Lower Palaeozoic times.

The composition and community structure of the world-wide *Hirnantia* faunas are seen to vary widely; some, e.g. the Bohemian assemblage, have as many as half of the taxa present consisting of endemic forms, yet other assemblages have no endemic species. Some assemblages have a relatively high diversity, with over thirty species of macrofauna recorded from them, and others have no more than five or six species in total, with perhaps only two or three abundantly represented (for a review of work up to that time see Cocks and Price 1975, pp. 720–723). The Oslo–Asker area is distinctive in showing most of the range of diversity in the different localities from which we have collected: the diversity of our *Hirnantia* faunas (including the *Hindella–Cliftonia* and *Dalmanella* Associations as well as the *Hirnantia* Association *sensu stricto*) differs from between two and thirty-four different species collected from each of the various localities. It is therefore probable that the variability in the diversity of the *Hirnantia* faunas recorded from various parts of the world is not necessarily caused by the more fundamental factors of geographical situation, but reflects partly the environmental location of the fauna and partly the variable conditions for colonization found on the local shallower shelf or lower shoreface. The stratigraphical appearance of the *Hirnantia* fauna seems to be closely correlated with the Hirnantian glacio-eustatic sea level changes. However, the suggestion that the *Hirnantia* fauna is a cold-water fauna (Sheehan 1979) should be treated with some caution in view of its great latitudinal spread which includes the circumpolar occurrences of what are now South Africa and Libya to the tropics of Canada, and its close association in the Oslo–Asker sequence with oolites which are usually associated with warm waters. Nevertheless it does seem that the late-Ordovician glacio-eustatic changes were connected with substantial changes in the community structure of the fauna, and with extinction of many species at the end of the Ordovician.

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DEVONIAN SHARKS FROM SOUTH-EASTERN AUSTRALIA AND ANTARCTICA

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ABSTRACT. Devonian shark remains from the Aztec Siltstone in south Victoria Land, Antarctica, are described as *Antarctilamna prisca* gen. et sp. nov., *Xenacanthus* sp., and *Mcmurdodus*? cf. *featherensis* White. Similar spines, teeth, and associated endocranial and jaw remains from the Bunga Beds on the far south coast of New South Wales are also referred to *A. prisca*. In this genus the teeth are diplodont, the fin-spines ctenacanthiform, and the braincase had a long otic region, prominent subocular shelves, and probably a persistent lateral occipital fissure. The double mandibular joint on the palatoquadrate resembles that of acanthodians. The other taxa are known only from isolated teeth. Both are freshwater occurrences of late Givetian to early Frasnian age. In a new hypothesis of interrelationships for early elasmobranchs, diplodont teeth are regarded as a synapomorphy of *Antarctilamna* and *Xenacanthus*, with the fin-spines of the former interpreted as a primitive feature. A ctenacanth origin for euselachians is rejected, and hybodonts and euselachians are considered to be closely related. A single dorsal fin and spine are interpreted as the primitive elasmobranch condition, shared with holocephalans, and the absence of spines in some Palaeozoic sharks is regarded as secondary.

FOSSIL shark remains from the Palaeozoic rocks of Australia have so far received little attention in the literature. The main references are Teichert's (1940, 1943) accounts of Permian bradyodont and *Helicoprion* teeth from Western Australia, the illustration of some Lower Carboniferous cladodont and bradyodont teeth from the Canning Basin by Thomas (1959), and Ørvig's (1969) brief mention of the occurrence of *Ohiolepis* scales in the Lower Devonian limestones from the Taemas/Wee Jasper region of New South Wales. These few reports give some hint of the diversity of early elasmobranchs awaiting discovery in the Australian region, and to these may be added the new material from south-eastern Australia and Antarctica described below. These new occurrences are in freshwater deposits of approximately the same age (late Middle/early Upper Devonian), and represent early records of another major group of elasmobranchs (the xenacanth sharks), which flourished in Carboniferous and Permian times. It is of interest that shark remains of similar age have recently been reported also from South America (Janvier 1978*a*) and Iran (Blieck *et al.* 1980).

SHARK REMAINS FROM THE AZTEC SILTSTONE, SOUTH VICTORIA LAND, ANTARCTICA

Woodward (1921) first described Devonian fish remains from moraine material derived from the 'Beacon Sandstone' of south Victoria Land, and the first *in situ* deposits were reported by Gunn and Warren (1962), and their material described by White (1968). Further localities in the same region of the Transantarctic Mountains were discovered in the summer field season of 1968–1969 by a geological expedition from the Victoria University of Wellington (McKelvey *et al.* 1972), and large collections were made by another Victoria University expedition in 1970–1971. These collections are currently being studied at the Australian Museum, Sydney, and the Bureau of Mineral Resources, Canberra (Ritchie 1971*a*, *b*, 1974, 1975; Young *in prep.*).

Woodward (1921, p. 56) tentatively referred various small dermal denticles in his material 'either to primitive Ostracoderms or to Elasmobranchs'. White (1968) identified a single small elasmobranch tooth for which he erected a new genus and species, *Mcmurdodus featherensis* White. Subsequently, Ritchie (in McKelvey *et al.* 1972) identified an elasmobranch tooth of completely different form, which he compared with *Xenacanthus*, in material from an important vertebrate locality in the Aztec

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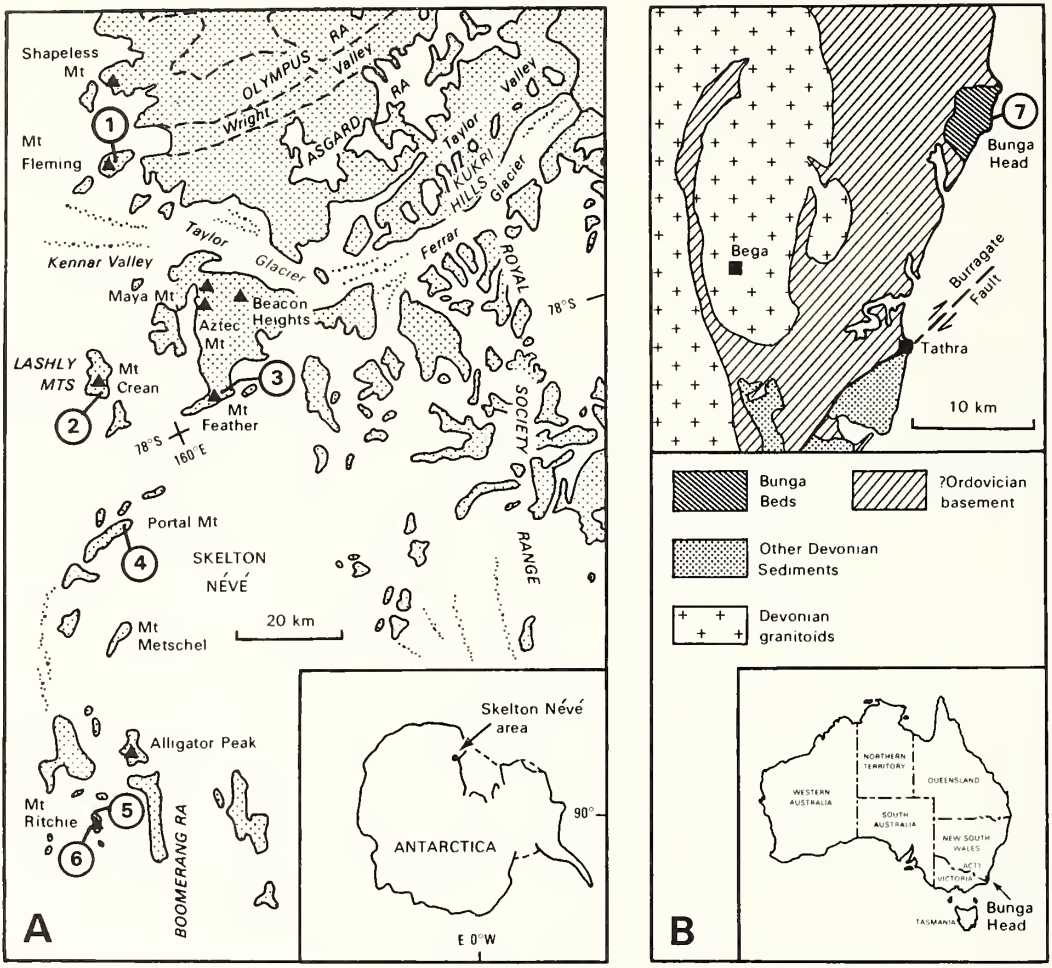


TEXT-FIG. 1. Localities (1–7) for the fossil shark remains described in this paper. A, outcrop map of the Skelton Névé region in the Transantarctic Mountains, south Victoria Land, Antarctica: B, generalized geology of the region around Bunga Head on the far south coast of New South Wales, Australia. Details of the numbered localities are given in the text.

Siltstone at Portal Mountain (text-fig. 1A). Further collecting in 1970–1971 yielded additional teeth from this locality, and teeth, spines, and scales from other localities including an incomplete, partly articulated specimen from the Lashly Mountains. With one exception, all this material comes from the Aztec Siltstone, the uppermost formation in the Devonian Taylor Group of the Beacon Supergroup (McKelvey *et al.* 1970, 1972, 1977; McPherson 1978). One elasmobranch spine (AMF 55550) comes from the underlying Beacon Heights Orthoquartzite at Mount Fleming.

Locality information for this material is as follows (numbers refer to text-fig. 1A). Horizons within the Aztec Siltstone are based on detailed sections reported in Askin *et al.* (1971) and Barrett and Webb (1973; see also McKelvey *et al.* 1977; McPherson 1978). Antarctic specimens described here which are housed in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra have been allocated numbers CPC 21187–21192 and 21214–21229. Other material is held in the Australian Museum, Sydney (prefix AMF), and the British Museum (Natural History), London (prefix P).

1. Mount Fleming. Beacon Heights Orthoquartzite exposed in the floor of the cirque east of Mount Fleming, 77° 32′ 43″ S., 160° 21′ E. (locality MS228 of McKelvey *et al.* 1972, 1977). One fin-spine referred to *Antarctilamna prisca* gen. et sp. nov. (AMF 55550) from near the top of the formation (Section 26, Barrett and Webb 1973).

2. Lashly Mountains. Section L1, Unit 8 of Askin *et al.* (1971). Southern end of low ridge extending south-east from Mount Crean, 77° 54·5′ S., 159° 34·5′ E. One specimen, the holotype of *A. prisca* (CPC 21187), from about 15 m above the base of the Aztec Siltstone.

3. Mount Feather. '300 ft above base of east ridge of Mount Feather, at junction of Ferrar and Skelton Glaciers, 77° 59′ S., 160° 30′ E.' (White 1968, p. 8). Locality MS7 of Gunn and Warren (1962). Holotype (P.49157) of *M. featherensis* White.

4. Portal Mountain. Section P1 of Askin *et al.* (1971), measured up the steep east-facing slope of the easternmost rock spur, 78° 7·2′ S., 159° 24′ E. Isolated scales and teeth (CPC 21188, 21189, 21191) from Unit 4, 7·1 to 15·9 m above the base of the Aztec Siltstone. One scale (CPC 21190) from Unit 14, 44·3 to 53·1 m above the base of the Aztec Siltstone. These specimens are referred to *A. prisca.*

Section 10 of Barrett and Webb (1973), measured up the south-facing slope of the easternmost rock spur, 78° 7·2′ S., 159° 23·5′ E. Fin-spine of *A. prisca* (AMF 55617) and various teeth of *Xenacanthus* sp. (CPC 21216–21227; AMF 54329–54331, 55573) from locality MS232 of McKelvey *et al.* (1972), which is Unit 17 of the measured section, 40·2 m above the lowest exposure of Aztec Siltstone. Fin-spine of *A. prisca* (CPC 21192) and teeth of *Xenacanthus* sp. (CPC 21214, 21215) from Unit 26, 70 m above the lowest exposure of Aztec Siltstone.

5. Near Mt. Ritchie. Lower part of Section A5 of Askin *et al.* (1971), measured up a rocky knoll at the northern end of a ridge running north from Mt. Kohn, 78° 31·7′ S., 158° 19·5′ E. One tooth of *Xenacanthus* sp. (CPC 21228) in greenish-grey siltstone.

6. Mt. Ritchie. Section A4 of Askin *et al.* (1971), measured up the east face from the edge of the Deception Glacier, 78° 32·2′ S., 158° 26′ E. One tooth (CPC 21229) in a loose piece of greenish-grey siltstone, probably from near Units 61 and 62. Described below as *M.*? cf. *featherensis* White.

SHARK REMAINS FROM THE SOUTH COAST OF NEW SOUTH WALES

These shark remains occur in the Bunga Beds, a circumscribed outcrop of Devonian sediments in the region of Bunga Head (text-fig. 1B), sitting unconformably on metaquartzites and slates of the (?) Ordovician Mallacoota Beds. This deposit has been interpreted as part of a complex system of Devonian volcanics and sediments which are widespread in the Eden–Pambula area (the 'Boyd Volcanic Complex' of Fergusson *et al.* 1979), and it is regarded as a lacustrine flysch deposit which accumulated in a rift-valley lake ponded against the nearby Burragate Fault (Fergusson *et al.* 1979, p. 93).

Fish remains in the Bunga Beds were first collected by Scott (1972) from a fossil plant locality at Bunga Beach (GR 2364E 59486N Murrah 1:25 000 Sheet; loc. 7, text-fig. 1B). These and a few subsequently collected specimens were briefly described in Fergusson *et al.* (1979, p. 102). At that time the characteristic diplodont teeth had not been identified in the material and the elasmobranch nature of these remains was not recognized. The locality was revisited in October 1979 and more elasmobranch fin-spines, many teeth, and a few other remains were collected. The associated fauna includes acanthodians and a holoptychoid rhipidistian, which also occur at two other localities higher in the Bunga Beds sequence. However, the shark remains are known only from the Bunga Beach locality, which is near the base of the sequence. At this locality they are the most common element in the fish fauna. Associated are abundant lycopod plants referred to the genera *Protolepidodendron* or *Lepidosigillaria* (see Gould 1975).

All the elasmobranch material from this locality is referred below to *A. prisca*. Specimens are housed in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (CPC 16994, 16995, 21193–21213), and the Geology Department collections at the Australian National University, Canberra (ANU 35333, 35334).

AGE AND CORRELATION

Since material referred to *A. prisca* comes from both the Antarctic and New South Wales localities, a tentative correlation may be proposed between the lower part of the Aztec Siltstone of south Victoria

Land, and the Bunga Beds of the New South Wales south coast. The age of the Bunga Beds has previously been assessed as 'no younger than early Frasnian, and probably Givetian' (Young *in* Fergusson *et al.* 1979, p. 103). The fish fauna in the Aztec Siltstone was initially regarded as Upper Devonian in age (Woodward 1921), but with better material White (1968, p. 6) favoured an age 'nearer the top of the Middle Devonian than the base of the upper . . .'. Subsequent work on the 1969–1971 collections now indicates some variation in the vertebrate assemblages through the Aztec sequence. Ritchie (1975, p. 571) has reported evidence of more than one species of the arthrodire *Groenlandaspis*, and there are several species of *Bothriolepis* (Young *in prep.*). Both genera occur right through the sequence, but some others (e.g. the placoderm *Phyllolepis* and the acanthodian *Gyracanthides*) appear to be restricted to upper levels. However, the elasmobranch material referred below to *Antarctilamna* comes mainly from the lower fossiliferous part of the sequence, being recorded from the upper beds of the Beacon Heights Orthoquartzite at Mt. Fleming, from 15 m above the base of the overlying Aztec Siltstone in the Lashlys, up to 53 m above the base in Section P1 (Askin *et al.* 1971) at Portal Mountain (a single scale), and probably at similar levels (two spines) in the adjacent Section 10 (Barrett and Webb 1973) at Portal. (Detailed correlation between the two Portal sections is uncertain, since in Section 10 the Aztec is some 40% thinner than in the nearby Section P1, the lower contact is not exposed, and the upper contact poorly exposed and probably disconformable.) The precise horizon of the holotype of *M. featherensis* is not known, but Helby and McElroy (1969, p. 379) imply that the Mt. Feather collections of Gunn and Warren (1962) came from near the top of the Aztec Siltstone. A single tooth tentatively referred below to *Mcmurdodus* sp. also comes from a high Aztec horizon in Section A4. The teeth described as *Xenacanthus* sp. are associated with *Antarctilamna* spines in Portal Section 10, and there is one tooth from the upper part of the Aztec Siltstone in Section A5.

To summarize, remains of *A. prisca* occur predominantly in the lower part of the Aztec Siltstone, and the other elasmobranchs appear to be restricted to the middle and upper parts, but whether this represents a faunal change through time or is facies controlled cannot be decided. It should be noted that the relevant lower beds of the Aztec at both the Portal and Lashlys localities are predominantly finely laminated lacustrine beds, this lithology being less common elsewhere.

In addition to the fish remains, a microflora from about 3 m below the top of the Aztec Siltstone at Aztec Mountain was described by Helby and McElroy (1969) as strongly reminiscent of assemblages from the Gneudna Formation of the Carnarvon Basin, Western Australia. They suggested a Frasnian age for the Aztec assemblage, although Seddon (1969) concluded on conodont evidence that the Gneudna Formation was slightly older than previously proposed, being of latest Givetian and/or earliest Frasnian age (see also Turner and Dring 1981). A less reliable maximum age for the Aztec is provided by lycopod remains from the underlying Beacon Heights Orthoquartzite, which have been dated as Lower–Middle Devonian (McKelvey *et al.* 1972, p. 348; see also Kyle 1977; Grindley, Mildenhall and Schopf 1980).

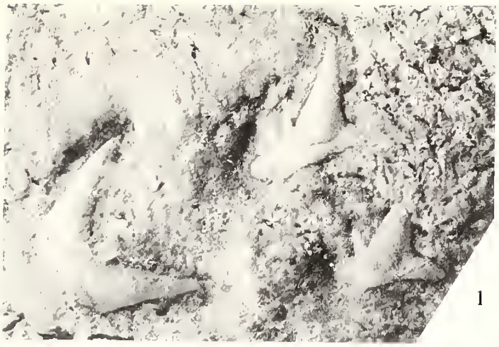
Taken together the evidence is thus consistent with a late Givetian/early Frasnian age for the Aztec fauna, which accords well with evidence from other early elasmobranch occurrences.

EXPLANATION OF PLATE 87

Figs. 1–10. *Antarctilamna prisca* gen. et sp. nov. 1, three teeth from piece *c* of the holotype, CPC 21187, ×6. 2, portion of ornamented fin-spine, AMF 55617 (latex rubber cast), ×6. 3, fin-spine, dorsal view, CPC 21205 (latex rubber cast), ×3. 4, fin-spine, dorsolateral view, CPC 21206 (latex rubber cast), ×3. 5, portion of fin-spine showing ornament, left lateral view, CPC 21204 (latex rubber cast), ×3. 6, 7, two scales in dorsal view from piece *j* of the holotype, CPC 21187, ×36. 8, scale in anterior view, with base preserved as an impression, piece *b* of the holotype, CPC 21187, ×24. 9, 10, dermal denticles from the branchial region, piece *d* of the holotype, CPC 21187, ×24. Figs. 1, 2, 6–10 from Aztec Siltstone, Lashly Mountains, south Victoria Land, Antarctica. Figs. 3–5 from Bunga Beds, Bunga Beach, south coast of New South Wales.

All specimens whitened with ammonium chloride.

PLATE 87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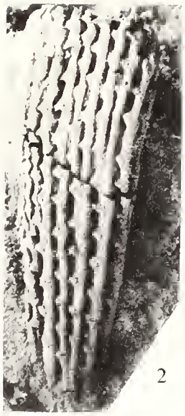
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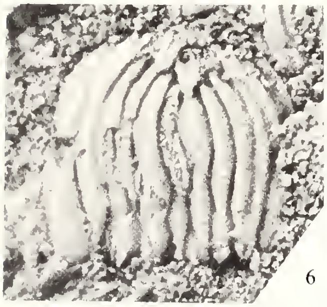
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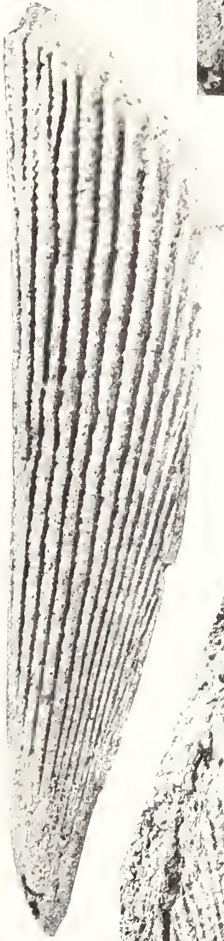
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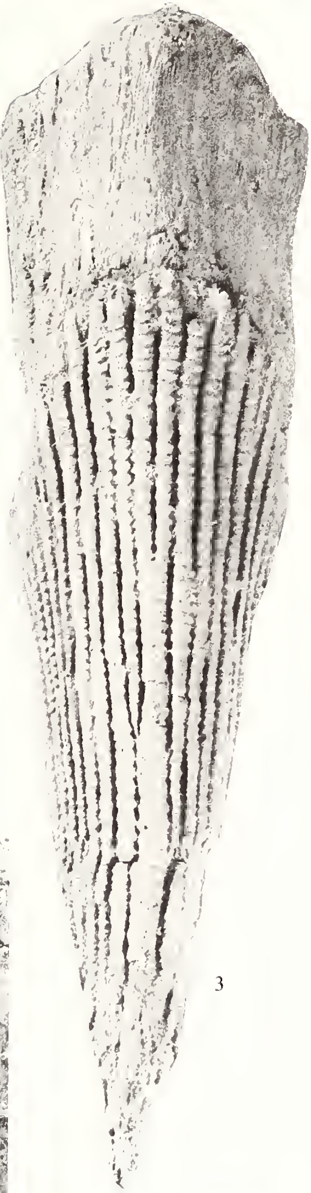
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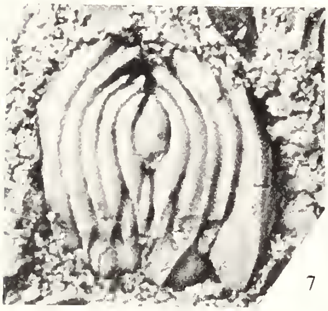
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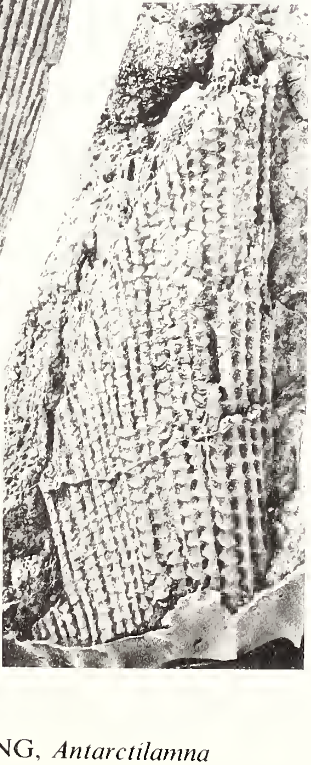
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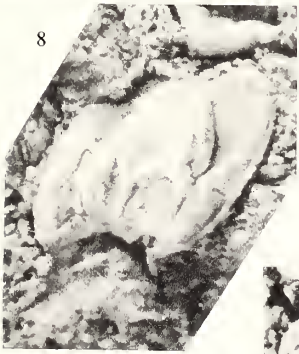
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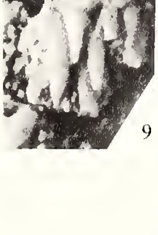
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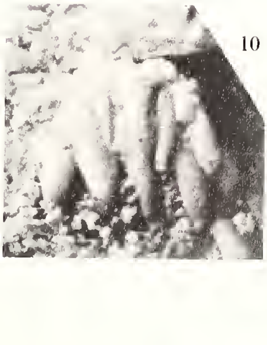
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YOUNG, *Antarctilamna*

Diplodont teeth referred to xenacanth sharks are first recorded elsewhere from the 'Genesee conodont bed' in New York State (Patterson *in* Andrews *et al.* 1967, p. 667), which lies at the base of the Genesee Group (Hussakof and Bryant 1918, p. 12). Rickard (1975) assessed these horizons as basal Frasnian, although evidence regarding the precise position of the Givetian/Frasnian boundary in this sequence is equivocal. The earliest ctenacanth spines noted by Patterson (*in* Andrews *et al.* 1967) occur in the underlying Hamilton Group in New York State, which is probably Givetian (Rickard 1975). These spines differ in various respects from those described below, but spines closely similar to this new material have recently been described from the Middle Devonian (?Eifelian) of Iran (Blieck *et al.* 1980; Janvier 1980). I conclude, therefore, that the lower part of the Aztec Siltstone may be late Givetian, and the upper part early Frasnian in age, and that available evidence strongly suggests a correlation with part or all of the Bunga Beds on the New South Wales south coast (the 'Flyschoid facies' of the Boyd Volcanic Complex—see Fergusson *et al.* 1979).

SYSTEMATIC PALAEONTOLOGY

Subclass CHONDRICHTHYES
Infraclass ELASMOBRANCHII
Genus *ANTARCTILAMNA* gen. nov.
Antarctilamna prisca sp. nov.

Plate 87, figs. 1–10; Plate 88, figs. 1–3, 5; Plate 89, figs. 5–8; text-figs. 2, 3A–D, 4–8.

1971*a*	*Gyracanthides* Ritchie, p. 16.
1971*b*	*Gyracanthides* Ritchie, p. 70.
1978	*Ctenacanthus* McPherson, p. 667.
1979	'endocranial casts . . . of a small placoderm . . .', 'large acanthodian spine with . . . tuberculate longitudinal ridges . . .'; Young *in* Fergusson *et al.*, p. 102.
1981	'elasmobranchs . . . with diplodont teeth and ctenacanth-like spines'; Young and Gorter, p. 90.

Etymology. From the Greek *antarktikos* (southern) and *lamna* (a kind of shark), and the Latin *priscus* (ancient).

Holotype. CPC 21187, a partly articulated incomplete specimen from the Lashly Mountains, south Victoria Land, Antarctica.

Other material. Isolated scales (CPC 21188–21190), teeth (CPC 21191), and spines (AMF 55550, 55555, 55617; CPC 21192) from Antarctica, and isolated teeth (CPC 21193–21202), spines (CPC 16995, 21203–21209; ANU 35334), endocrania (CPC 16994, 21210, 21211; ANU 35333, 35334) and jaw remains (CPC 21212, 21213) from the Bunga Beds, south coast of New South Wales, Australia. (For locality details see above.)

Definition. Elasmobranchs with probably five gill openings; braincase with a long otico-occipital division, small postorbital and larger lateral otic processes, extensive subocular shelf and probably a persistent lateral occipital fissure; teeth diplodont with up to three mesial cusps and a lingual torus; lateral cusps curved in a single plane and directed lingually. Palatoquadrate with both pre- and postarticular processes for the mandibular joint, the former with an articular depression on its lateral

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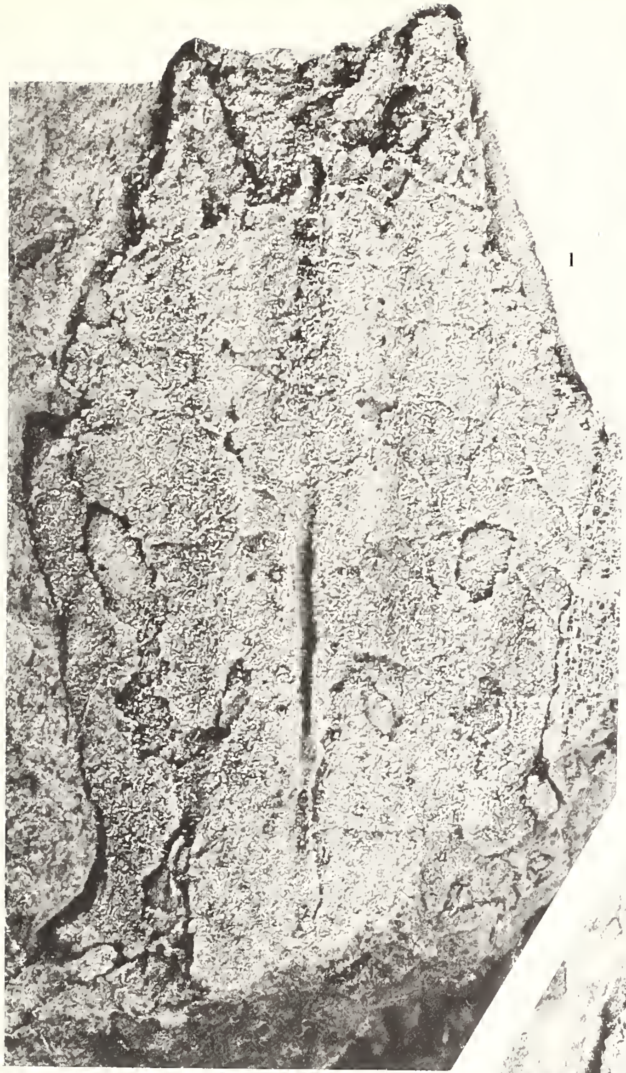
EXPLANATION OF PLATE 88

Figs. 1–3, 5. *Antarctilamna prisca* gen. et sp. nov. 1, 5, endocranial casts (ANU 35333, CPC 16994) in ventral view, Bunga Beds, Bunga Beach, south coast of New South Wales, × 3. 2, 3, incomplete left palatoquadrate in lateral and mesial views, CPC 21212 (latex rubber cast), locality and horizon as for figs. 1, 5, × 1.

Fig. 4. *Mcmurdodus*? cf. *featherensis* White. Isolated tooth (CPC 21229), with base preserved mainly as an impression, Aztec Siltstone, Mt. Ritchie, south Victoria Land, Antarctica, × 4.

All specimens whitened with ammonium chloride.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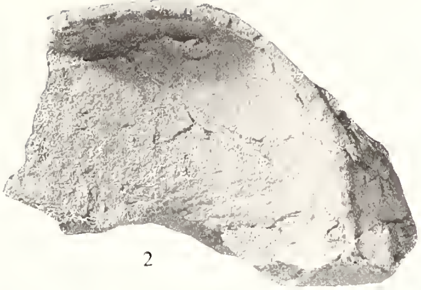
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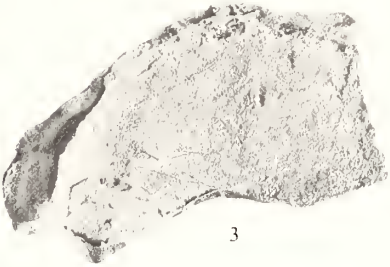
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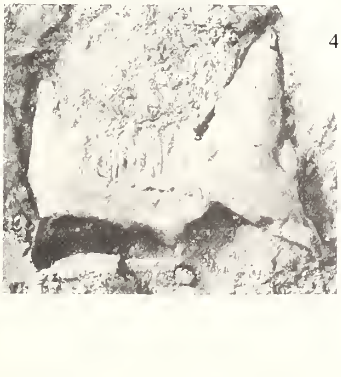
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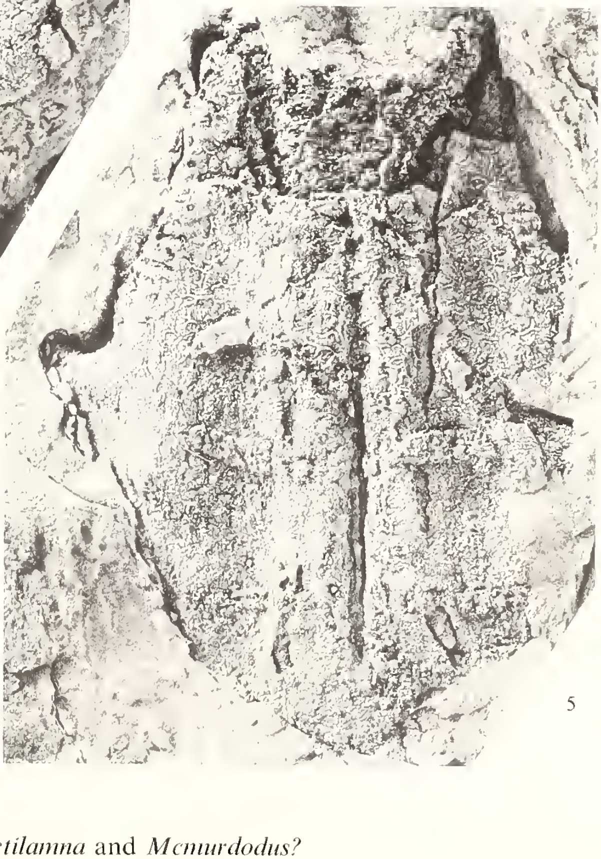
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YOUNG, *Antarctilamna* and *Mcmurdodus?*

face. Probably two dorsal costate fin-spines, triangular in cross-section with a large central cavity posteriorly placed, and a small inserted portion; scales compound, with a flat crown ornamented with concentric ridges, and a cup-shaped base.

Remarks. The single elasmobranch tooth previously described from the Aztec Siltstone by White (1968) as *Mcmurdodus featherensis* shows no resemblance to the teeth of this new form. As far as could be observed in the holotype and in other specimens, the teeth of *Antarctilamna prisca*, apart from size, show little variation, a common feature of Devonian elasmobranchs, even though some degree of heterodonty has recently been described in the Lower Carboniferous form *Tristychius* (Dick 1978). It is surprising that several freshwater sharks with such distinctive dentition should coexist in the Aztec Siltstone, and that no definite further remains of *M. featherensis* have yet been identified. Since, however, there is no evidence of variation in tooth morphology in the articulated specimen described below, and as far as is known heterodonty is not a feature of other Devonian elasmobranchs, this specimen has been designated the holotype of a new species in a new genus, to which a few isolated scales, teeth, and incomplete spines from Portal Mountain and Mt. Fleming may be referred. The elasmobranch material from the Bunga Beds is regarded as conspecific on the evidence of associated teeth and spines which cannot be distinguished in any significant details from corresponding elements in the Antarctic material.

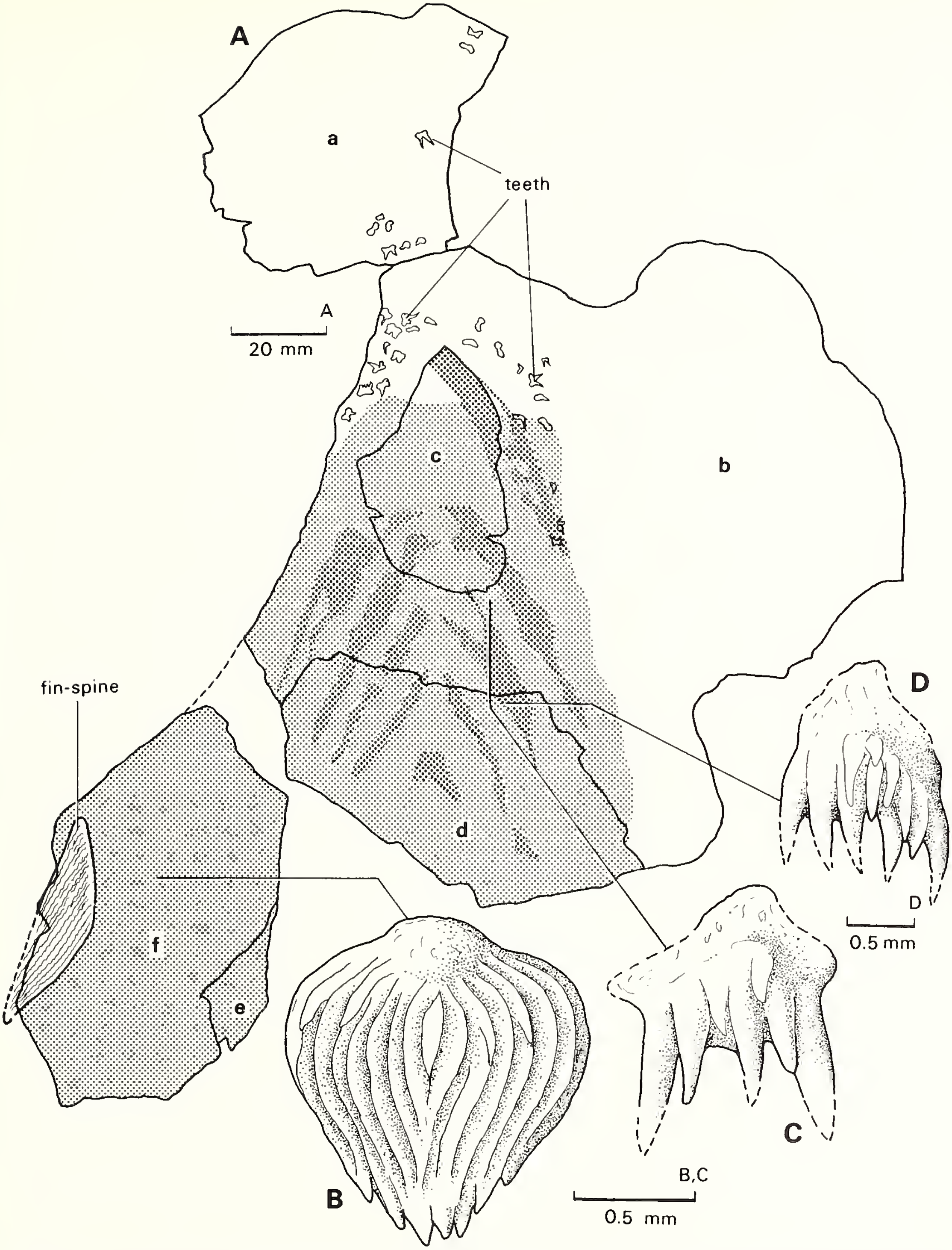
Description. The holotype is preserved in six main pieces of a flat nodule of fine calcareous siltstone which was incomplete and separated when collected. The largest piece (*b*, text-fig. 2) has two smaller pieces as counterparts (*c*, *d*), and pieces *e* and *f* are also part and counterpart, but their relationship to the other pieces is uncertain. The bedding plane containing the fish is partly enclosed in piece *a*, with broken teeth and scales exposed around its convex margin. In addition, there are three smaller pieces (labelled *g*, *h*, *j*) associated with *e* and *f*, and various small flakes displaying fragments of teeth or shagreen patches.

Despite its incompleteness, a general orientation for the specimen has been determined. Teeth are scattered around the anterior end of piece *b* (as oriented in text-fig. 2), and around the margins of piece *a*, indicating proximity to the head region and mouth. Most of the area of shagreen on piece *b* displays a pattern of irregular but apparently symmetrical undulations converging anteriorly, which I interpret as ventral extensions of the gill openings. Some of these elongate depressions contain patches of a granular material, possibly remains of the ceratobranchials, and it is assumed therefore that the area of shagreen on piece *b* represents a visceral view of the ventral surface of the branchial region. Consistent with this interpretation is the imbrication of surrounding denticles, each overlapping the one behind. In the branchial region these are aligned parallel to the branchial arches.

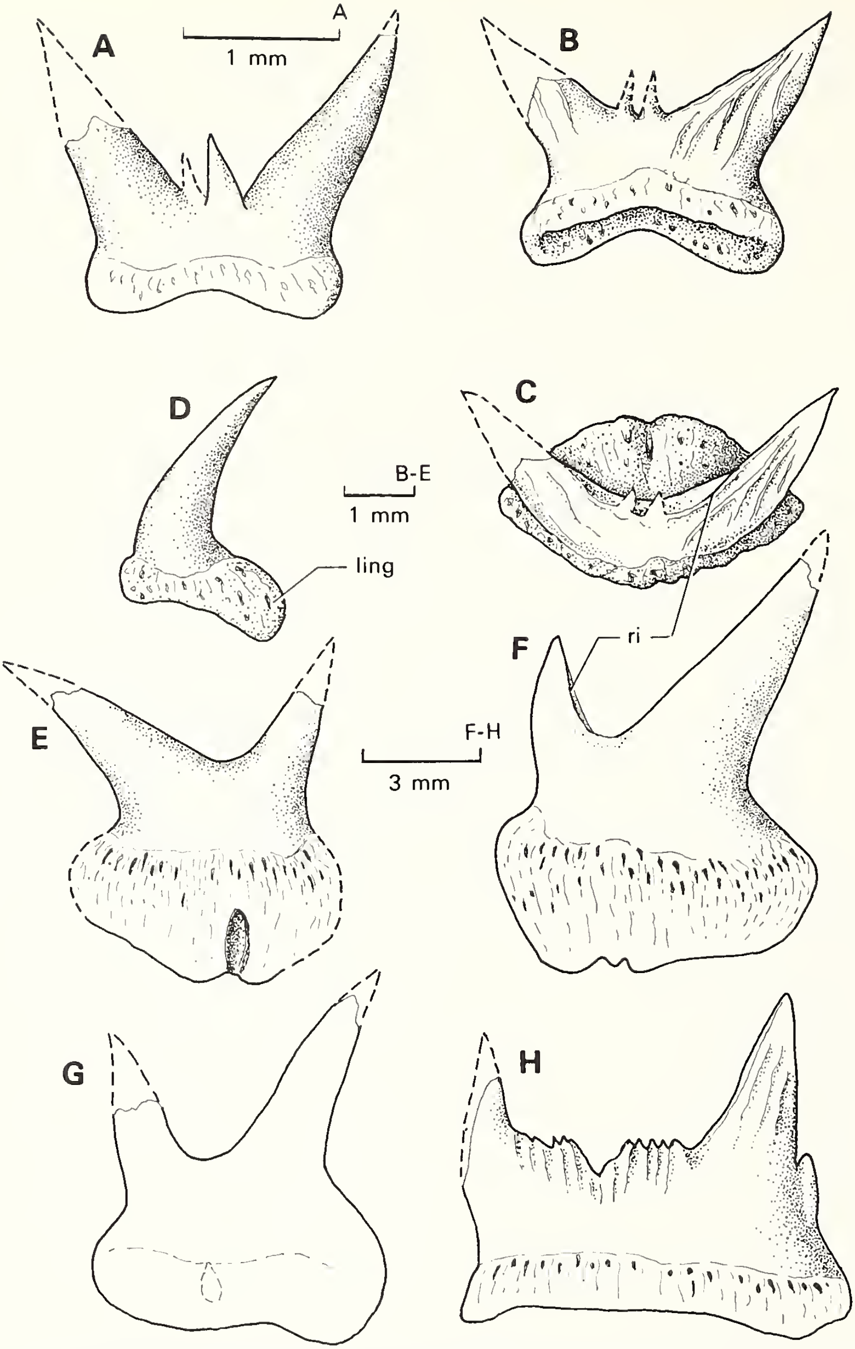
The texture of the outer surface of piece *e* shows that it is also from the ventral side of the nodule. A fin-spine is partly preserved at the edge between pieces *e* and *f* and presumably represents the dorsal midline of the fish. The orientation of the spine and the alignment and imbrication of surrounding denticles suggest an approximate position for pieces *e* and *f* relative to pieces *a* and *b* as shown in text-fig. 2, the fish having been compressed in the nodule with the dorsal spine folded over to the left side. Thus interpreted, a considerable portion of the specimen is missing, and little can be deduced of general body form and fin shape. The specimen is of major significance, however, in demonstrating scale, fin-spine, and tooth morphology within a single species.

Teeth. About sixty-five teeth or parts thereof are visible on the articulated specimen, and isolated teeth are common in the Bunga material. The teeth in CPC 21187 vary in size, a large tooth (text-fig. 3A) being about 4 mm across the root, with cusps about 2·5 mm long. One of the smallest visible teeth (on piece *b*) is slightly under 1 mm wide across the root. For most of the teeth this measurement is about 3 mm.

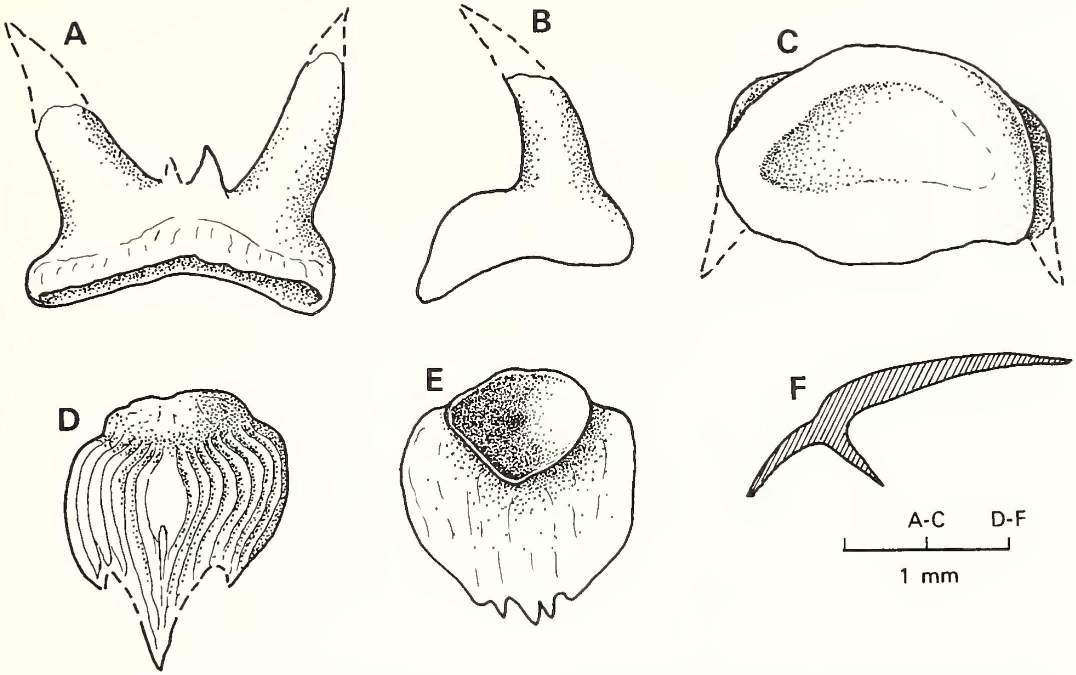
All teeth are of diplodont type, with two prominent, curved lateral cusps separated by two or three much smaller mesial cusps. Where there are three subsidiary cusps the central one may be slightly larger (Pl. 87, fig. 1), but it does not approach the size of the lateral cusps, and in this respect this species differs from teeth previously described by Hussakof and Bryant (1918, fig. 51B, C) as *Dittodus priscus* (Eastman), or those named by Wells (1944) as *Phoebodus* (e.g. Gross 1973, pl. 34, fig. 15). The crown and its cusps have a shiny enameloid-like surface. The cusps may be smooth (text-fig. 3A), or more commonly striated (text-fig. 3B, C), the striations tending to spiral slightly towards the tip. The number of striations varies but typically about six are exposed on the labial surface. They are not as strongly developed as the striations on *D. priscus* (see Hussakof and Bryant 1918, pl. 44, fig. 3). The only tooth with the lingual surface of the cusps clearly exposed (on the edge of piece *c*) is smooth here, so the striations may have been restricted to the outer surface, as these authors have described (Hussakof and Bryant 1918, p. 145). The striation lying in the plane of the mesial cusps may be slightly



TEXT-FIG. 2. *Antarctilamna prisca* gen. et sp. nov. Holotype (CPC 21187), a partly articulated specimen from the Lashly Mountains, showing (A) the six main pieces from the nodule (labelled *a–f*), and illustrating some variation in the size and morphology of denticles from different regions of the specimen (B–D). Extent of shagreen shown by stippling. Granular material, possibly representing remains of ceratobranchials, densely stippled.



TEXT-FIG. 3. A–D, *Antarctilamna prisca* gen. et sp. nov. Teeth from the holotype, CPC 21187. A, B, from piece *a* (see text-fig. 2) in labial view. C, D, dorsal and posterior views showing curvature of the cusps (restored after several teeth). E–G, *Xenacanthus* sp. E, CPC 21215 from Portal Mountain, Section 10, Unit 26, lingual view. F, CPC 21224 from Portal Mountain, Section 10, Unit 17, lingual view. G, CPC 21228 from near Mt. Ritchie, lower part of Section A5. Outline shape only of this tooth, which is abraded, and preserved partly as an impression in labial view. Position of the pore on the lingual surface indicated by a dashed line. H, *Mcmurdodus*? cf. *featherensis* White. CPC 21229 from Mt. Ritchie, Section A4, near Units 61 and 62. *ling*, lingual torus; *ri*, ridge on cusps forming a cutting edge.



TEXT-FIG. 4. *Antarctilamna prisca* gen. et sp. nov. A–C, restoration of a tooth from the Bunga Beds (CPC 21198) in labial, posterior, and ventral views. D, an isolated trunk scale from Portal Mountain, Section P1, Unit 14 (CPC 21190). E, sketch restoration of a scale in basal view, after various broken scales on pieces *c*, *e*, *h*, and *j* of the holotype (cf. Pl. 89, fig. 6). F, vertical midline section through a scale, restored after various scales on piece *e* of the holotype.

accentuated as a thin cutting-edge on the adjacent basal parts of the lateral cusps (*ri*, text-fig. 3C). Otherwise the cusps are circular in cross-section.

The root of the tooth is always clearly delineated from the crown, being composed of the cancellous bone-like tissue typically seen in elasmobranch teeth. Its basal surface is distinctly concave, and there is a lingual torus (*ling*, text-fig. 3D), which in one broken tooth removed from the matrix has a slight swelling on its dorsal surface corresponding to the 'button' structure figured by Hussakof and Bryant (1918, pl. 44, fig. 3A, B). Two other examples (from near the left margin of the anterior end of piece *b*) have a slight depression here, and an elongate opening slightly larger than surrounding pores in the basal tissue (text-fig. 3C). A corresponding large pore is seen in examples of *Phoebodus politus* Newberry figured by Gross (1973, pl. 34, figs. 13*a*, 14, 16, 21). In most instances the curvature of the cusps on these teeth in relation to the morphology of the root could not be determined because of incomplete preservation. However, in the examples illustrated in text-fig. 3B and Pl. 87, fig. 1, there is no doubt that the cusps curved to the lingual side. The opposite curvature is indicated for other teeth referred below to *Xenacanthus* sp.

None of these teeth has been sectioned, but several broken examples show the cancellous basal tissue occupying the core of the lower part of the cusp, and surrounded by a compact lamellar tissue, presumably dentine. Above this a thin pulp cavity extends to the tip of the cusp.

Teeth in the Bunga Beds material (text-fig. 4) are all of similar size and form, but less well preserved. Invariably the original tissue has disappeared and they have been studied using latex rubber moulds. Of the ten teeth studied, CPC 21195 and 21200 show clearly at least one small intermediate cusp, possibly flanked by additional, more diminutive cusps. In CPC 21198 the concave ventral surface of the base, the curvature of the cusps, and the extent of the lingual torus are all well shown (text-fig. 4A, B, C). The concave base is also seen in CPC 21196, and CPC 21201 shows a swelling on the dorsal surface of the torus similar to that described above. Only one tooth (CPC 21195) shows striations on the cusps, but their absence may be attributed to the inferior preservation, and no other significant differences from the teeth in the Antarctic material are apparent.

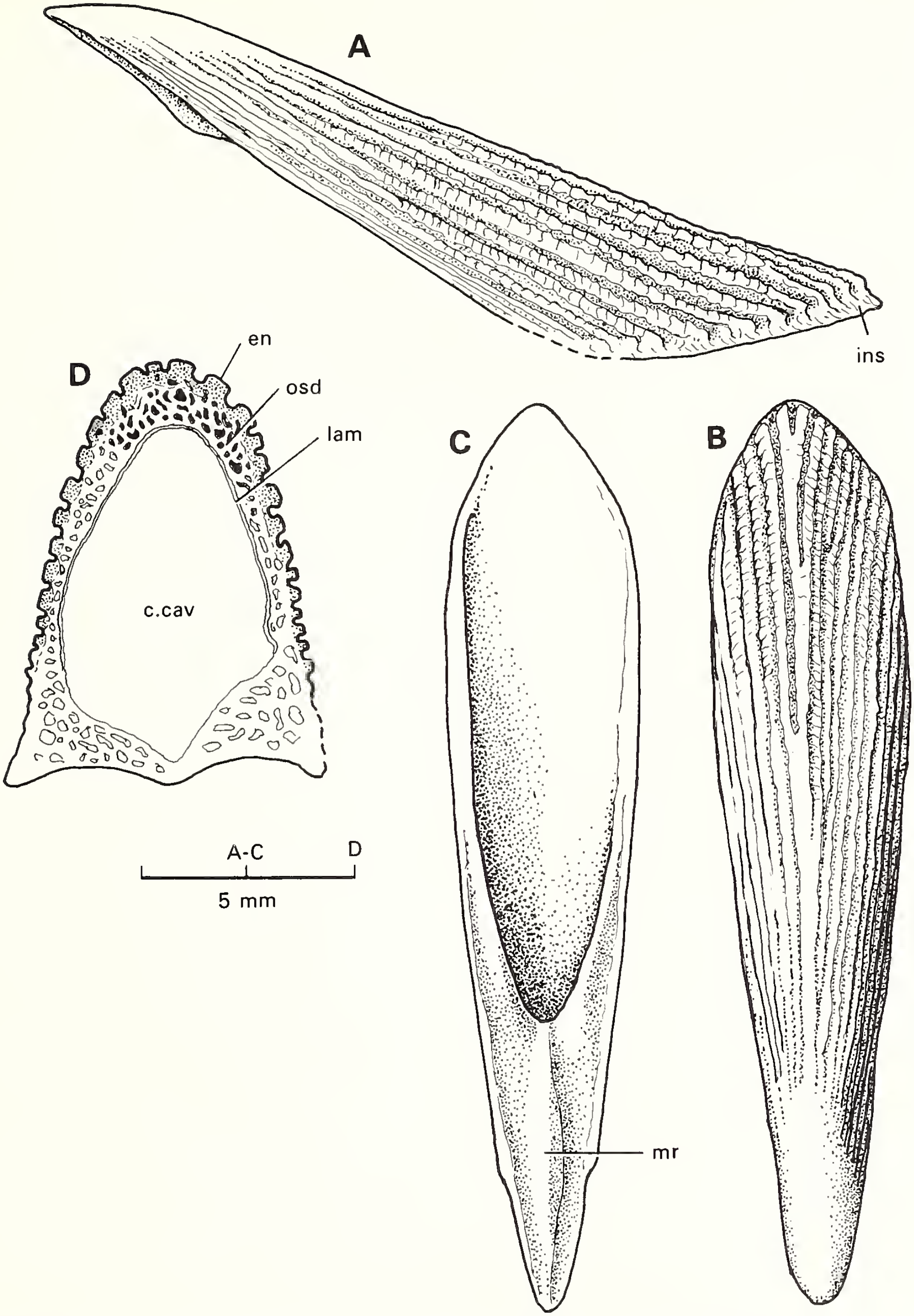
Fin-spines. Teeth of the diplodont form just described have long been recognized to belong to a shark bearing a single, barbed cephalic spine of the type named *Xenacanthus* by Beyrich (see Woodward 1889, p. 2). These spines are elongate, straight, subcircular to subelliptical in cross-section, and bear two rows of denticles (e.g. Davis 1880). Similar spines, but lacking the denticle rows, were named *Anodontacanthus* by Davis (1881), although Traquair (1888) pointed out that the absence of denticles in this case could be attributed to wear. The earliest recorded xenacanth spine, also named *Anodontacanthus*, came from the Middle–Upper Devonian 'Genesee conodont bed' (Andrews *et al.* 1967, p. 667), and Hussakof and Bryant (1918, p. 157) commented that the occurrence with *Dittodus* teeth from the same horizon was to be expected, such teeth also being recognized as belonging to xenacanth sharks.

It is of some interest therefore that the spines described below are of completely different form, resembling in several respects those of another group of early sharks, the ctenacanths. That the teeth and spines described here belong to one species is established by the spine in CPC 21187 (text-fig. 2), which, although somewhat flattened, has the same short, broad form as disarticulated spines in the Bunga Beds material. The latter are well represented in the collection, and provide the basis for a fairly complete description of fin-spine morphology. All are relatively short and broad, with little curvature (text-fig. 5; Pl. 87, figs. 3, 4). They are readily distinguished from early North American examples of ctenacanth spines, which are more slender (e.g. *Ctenacanthus wrighti* Newberry, 1889, pl. 26, fig. 4), or slender and curved (e.g. *C. nodocostatus* Hussakof and Bryant 1918, pl. 51, fig. 1). However, a similar overall form is shown by a recently figured spine with ctenacanth ornament from the Eifelian of Iran (Blieck *et al.* 1980, pl. 1, fig. 20).

All spines bear strong longitudinal costae, which when well preserved and unworn exhibit the cone-in-cone type ornament characteristic of ctenacanths. In detail the ornament shows some variation, with the separation of nodes along each costa approximating their width in the holotype and CPC 21192, but being more widely spaced in another spine fragment from Antarctica (Pl. 87, fig. 2). The Bunga spines show less variation, but are generally more poorly preserved. However, in CPC 21204 the ornament is well shown (Pl. 87, fig. 5), and appears identical to that on the spine of the holotype. In many specimens the costae are worn down to a smooth area on the anterior margin near the tip of the spine (text-fig. 5B). The number of costae varies considerably; in 11 spines from Bunga there may be as few as about 15 or as many as 26 costae per side, reducing to between 6–10 near the tip of the spine. Costae near the posterolateral borders of the ornamented area become much finer and more closely spaced. Similar variation is indicated in the Antarctic material, with about 16 costae on one side of CPC 21192 but at least 25 on the spine of CPC 21187. There is some coalescence of costae along the anterior margin (e.g. CPC 21192, 21206), but they are otherwise fairly continuous. Typically there is a very narrow zone of insertion along the spine base (*ins*, text-fig. 5A), again a point of resemblance to the figured specimen from Iran, and clearly different in this respect from other ctenacanthiform spines. The spine must have been only loosely attached in the skin, as in *Cladoselache* (see Harris 1938). This was probably the primitive condition. However, in two Bunga specimens (CPC 21205, 21208) the inserted portion of the spine is more extensive (Pl. 87, fig. 3), and it is likely therefore that there were spines anterior to both dorsal fins, the posterior being more deeply inserted into the body musculature. In all spines examined the edge of the inserted portion makes a fairly constant angle (about 35°) with the anterior border of the spine.

The posterior surface of the spine is well displayed in CPC 16995, and is partly visible in CPC 21206. It is slightly concave, with elevated lateral rims (text-fig. 5C), and a low median ridge extending from near the tip to the distal end of the basal opening. In CPC 21206 the ridge is sufficiently prominent to be visible in lateral view. The basal opening occupies about 50% of the length of the spine in CPC 16995, and slightly more (about 60%) in CPC 21206. There is no sign of posterior denticle rows, said to be typical of ctenacanth and sphenacanth spines by Woodward (1889, p. 241; but cf. Maisey 1978, p. 658).

A section through a spine associated with CPC 21206 was exposed in trimming this specimen with a saw (text-fig. 5D). It may be an oblique section, passing through the spine probably just above the basal opening, but nevertheless indicates the triangular form seen in some (but not all) ctenacanth spines (Maisey 1977, p. 265; cf. Newberry 1889, pl. 26, fig. 1). Blieck *et al.* (1980, p. 146) have commented that the elasmobranch spines from Iran are atypical in their 'rounded anterior edge', and this could also be said of the spines described here. The hard tissue of the sectioned spine is partly weathered, but some significant features can be made out. Lining the large central cavity (*c.cav*) is a thin compact layer (*lam*), presumably the lamellar inner layer of dentine reported by Maisey (1977, p. 263) to occur distally in ctenacanth spines. Surrounding this is a zone of trabecular osteodentine traversed by numerous canals, many of which have a thin lining of compact tissue similar in appearance and its whitish colour to the lamellar lining of the central cavity. The trabecular structure extends into the costae, although these are differently stained (indicated by stippling in text-fig. 5D). Whether this differential staining indicates outer and inner osteodentine zones is uncertain, and needs confirmation on better material. A thin dark outer layer (*en*) is interpreted as vitrodentine investing the surface of the costae and the intercostal furrows.



TEXT-FIG. 5. *Antarctilamna prisca* gen. et sp. nov. Fin-spines from the Bunga Beds. Restoration in lateral (A), dorsal (B), and ventral (C) views, after CPC 16995 and 21206 (cf. Pl. 87, fig. 5). D, section through fin-spine, CPC 21207. *c.cav*, central cavity of spine; *en*, possible vitrodentine layer; *ins*, inserted portion of spine; *lam*, lamellar dentine; *mr*, median ridge; *osd*, trabecular osteodentine.

Finally, the section clearly indicates the form of the posterior wall of the spine, which is fairly thin and concave. The triangular cross-section, the posterior position of the central cavity, the thinner concave posterior wall, and the absence of posterior denticle rows are all features by which ctenacanth spines are distinguishable from hybodont spines according to Maisey (1975, 1977, pp. 263–265). The significance of these resemblances is considered below.

Scales. No scales have been identified in the Bunga material, and apart from a few isolated scales in the Portal Mountain collection, the following account is based entirely on CPC 21187, in which scales are generally excellently preserved (Pl. 87), although detail is often obscured by their close imbrication. In addition the nodule has split through the interior of most scales, necessitating some mechanical preparation to determine external morphology. The scales vary in size, the largest (about 1·5 mm across) occurring on pieces *e* and *f* (text-fig. 2), presumably from the dorsolateral parts of the trunk region. In the ventral midline immediately behind the branchial region on piece *b* they are slightly smaller (about 1·3 mm across), and considerably smaller scales (0·5–0·9 mm across) are associated with the scattered teeth and remains of the ceratobranchials. Zangerl (1968) has recorded a similar size-variation from larger dorsal to small ventral scales in the Carboniferous shark *Orodus*.

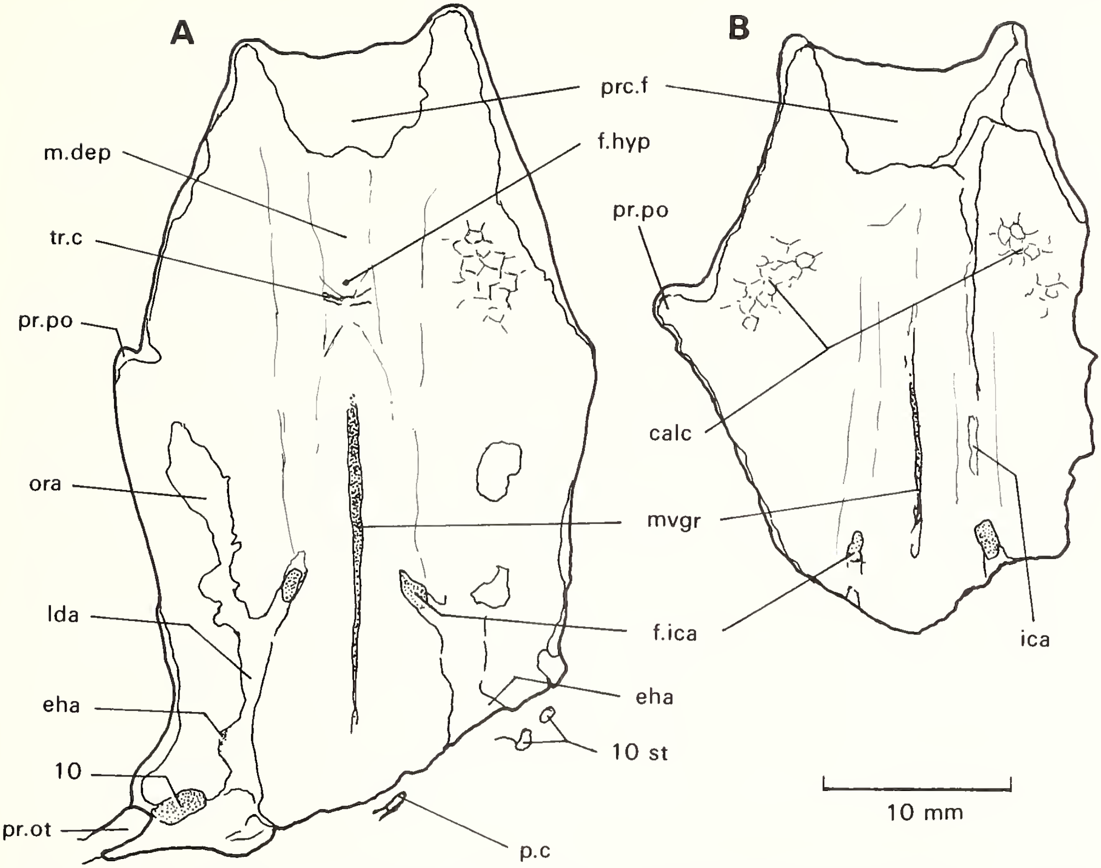
The typical trunk scales which predominate in the specimen have a characteristic morphology which is well displayed on both sides of two small flakes (labelled *h* and *j*) from between pieces *e* and *f*. The isolated scales from Portal Mountain (CPC 21188, 21190) have a similar morphology. The scale crown is fairly flat, and ornamented with a series of concentric ridges (commonly six to eight on each side) arising near the anterior margin, and converging posteriorly where they may be extended as short cusps along the posterior margin (text-fig. 2B). Anteriorly the ridges may carry subsidiary grooves (Pl. 87, figs. 6, 7), in this respect resembling *Cladolepis* scales (see Gross 1973, pls. 31–33). Many scales in CPC 21187 are broken or weathered to expose their concentric inner structure, as first described by Gross (1938, fig. 5M). In others the separate pulp cavities within each ridge are clearly seen, the ridges thus corresponding to the individual denticles or odontodes which make up the composite scales of other Palaeozoic elasmobranchs (Ørvig 1966; Zangerl 1966, 1968). The base of the scale is not well shown, but sections through imbricated scales along the edge of piece *e* immediately adjacent to the fin-spine (text-fig. 4F) are reminiscent of Zangerl's figure (1968, fig. 2) for *Orodus*. In *Orodus* the scale base is described as comprising two bony projections which were embedded in the dermis at right angles and parallel to the surface of the skin (Zangerl 1968, p. 401). In these scales, however, it is clear that the base was a deeply concave, cup-shaped structure (text-fig. 4E; Pl. 89, fig. 6) attached by a constricted neck to the scale crown. A central pore possibly opened into the coalesced pulp cavities of the denticles making up the crown. This morphology is in marked contrast to the thickened cushion-like base seen in scales of *Protacrodus*, *Ohiolepis*, and *Cladolepis* (e.g. Gross 1973, pls. 30–32).

In addition to these typical trunk scales there are a small number of other scales with more discrete denticles on the crown, which seem to be restricted to the gill-arch and mouth region of the specimen. In these scales (text-fig. 2C, D; Pl. 87, figs. 9, 10) the crown comprises a cluster of posteriorly directed, finger-like denticles, somewhat similar to the compound scales of *Orodus* figured by Zangerl (1968, fig. 1). These must correspond to the branchial teeth described in other xenacanths (e.g. Glikman 1964, figs. 21, 22).

Nothing exactly similar to the dermal tubercles described by Woodward (1921, pp. 56–57) has been identified in the new material. Some of these were reported to have a large pulp cavity, which led Gross (1950, p. 72) to suggest that they were agnathan remains (psammosteids). In others Woodward mentioned a microscopic structure which was 'typically Elasmobranch', with traces of a separate pulp cavity within each cusp of the scale, as described above. These latter scales possibly belong to *Antarctilamna*.

Braincase. One of the more interesting aspects of this new material is the presence of endocranial remains in the Bunga Beach specimens. These are perhaps the earliest known shark braincases, although (probably) slightly younger examples have long been known from the early Upper Devonian of Wildungen, Germany (Gross 1937, 1938; Stensiö 1937). Their close association with the teeth and spines described above indicates that these braincases probably belong to *Antarctilamna*, although conclusive evidence (e.g. articulated specimens) is lacking. All five examples are preserved in ventral view as dorsoventrally compressed casts, presumably formed by the infilling of fine sediment after the decomposition of cartilage. A hexagonal pattern of fine ridges on parts of CPC 16994 and ANU 35333 (*calc*, text-fig. 6B; Pl. 88, figs. 1, 5) may be an impression of the original prismatic surface calcification. Some internal canals are also preserved as sediment infills, and it is likely that detailed information on internal structure will be forthcoming when additional specimens are available for study. Such detailed preparation and examination is beyond the scope of this preliminary account, but some attempt has been made to interpret canals and foramina visible externally.

The most informative specimen is ANU 35333 (text-fig. 6A; Pl. 88, fig. 1), in which all the endocranial processes

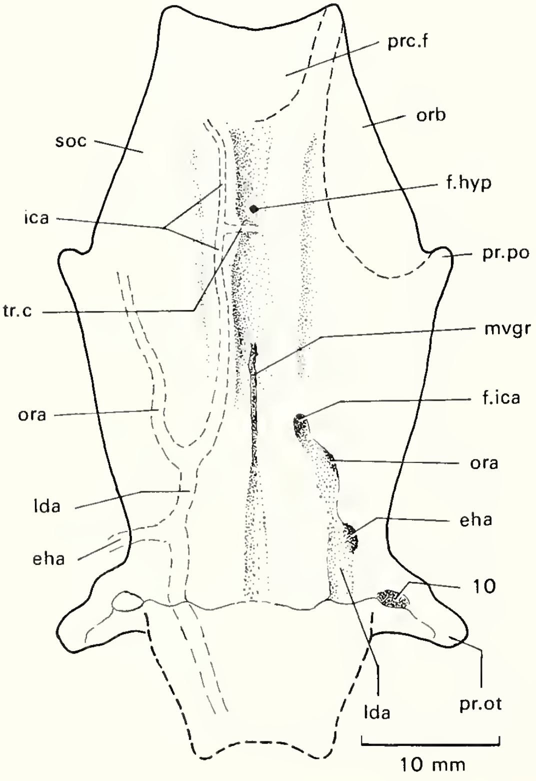


TEXT-FIG. 6. *Antarctilamna prisca* gen. et sp. nov. Braincases from the Bunga Beds in ventral view. A, ANU 35333 (cf. Pl. 88, fig. 1); B, CPC 16994 (cf. Pl. 88, fig. 5). *calc*, impressions of prismatic calcified cartilage; *eha*, canal for efferent hyoidean artery; *f.hyp*, possible buccohypophysial foramen; *f.ica*, foramen or canal for internal carotid artery; *ica*, canal for internal carotid artery; *lda*, canal or groove for lateral dorsal aorta; *m.dep*, median depression; *mvgr*, median ventral groove; *ora*, canal for orbital artery; *p.c*, canal, possibly for a spino-occipital nerve, or for the occipital artery; *prc.f*, precerebral fontanelle; *pr.ot*, lateral otic process; *pr.po*, postorbital process; *tr.c*, canal possibly connecting the internal carotid canals of each side; *10*, foramen, possibly for vagus nerve; *10 st*, foramina, possibly for the supratemporal branch of the vagus nerve.

of one side are preserved. In this and another specimen (Pl. 88, fig. 5) an anterior notch is assumed to represent the precerebral fontanelle (*prc.f*, text-figs. 6, 7), its floor having broken away. The right postorbital process is clearly preserved in both specimens (*pr.po*, text-fig. 6), and in ANU 35333 there is also the remnant of a prominent lateral otic process (*pr.ot*). The ventral midline of the braincase is marked by a deep groove (*mvgr*) separating conspicuous paired foramina near the posterior end (*f.ica*). Each foramen lies at the anterior end of a shallow groove extending from the posterior preserved margin (the nature of the preservation suggests that this groove may in part have been a canal which has lost its thin ventral wall). A pair of low ridges extend anteriorly from these foramina, separated by a shallow median depression in which a possible buccohypophysial foramen has been identified in ANU 35333 (*f.hyp*, text-fig. 6A). That these ridges contain paired canals extending almost to the precerebral fontanelle is shown by CPC 16994 and 21211 (text-fig. 6B; Pl. 88, fig. 5; Pl. 89, fig. 5), where the canal floor has broken away. CPC 21211 shows a large lateral branch behind the main foramen, also seen on the right side of ANU 35333 (left side of Pl. 88, fig. 1), whilst on the left side of ANU 35333 a more posterior lateral branch is indicated (*eha*, text-fig. 6A).

This canal system can only be for the paired lateral dorsal aorta and its various branches. The partial enclosure of these arteries in the braincase floor is probably a primitive gnathostome feature (e.g. Gardiner 1973, p. 111), and the condition has been noted in many Palaeozoic elasmobranchs (Romer 1964; Schaeffer 1967). In such forms, however, the main arteries derived from the lateral dorsal aorta (the efferent hyoidean and orbital arteries) normally emanate from the anterior end of a fairly long aortic canal, and a considerable distance in front of the occiput (e.g. Schaeffer 1981, fig. 12). In contrast, ANU 35333, which is the only specimen with an apparently natural posterior margin partly preserved, has these branches located near the posterior end of the main length of aortic canal. This condition could be due to the relatively long otic and almost completely reduced occipital segment of the braincase in this form. Nevertheless, these branches are similarly placed, relative to the postorbital and otic processes, to those figured for *Xenacanthus* by Schaeffer (1981, fig. 12A), and since even in early elasmobranchs with the otico-occipital region reduced (e.g. *Cladoselache*) the occipital segment projects out behind the otic processes, I suggest that the occipital segment has been lost from this specimen. In *Tamiobatis*, Romer (1964, p. 97) noted a break in surface calcification at the base of the otic process, and a similar condition may have obtained in *Antarctilamna*. An occipital segment has been restored in text-fig. 7. The reconstruction is generally comparable in overall proportions to that for *Xenacanthus*, but with a broader otic region behind the postorbital processes (which are less prominent), and with more pronounced subocular shelves, of similar extent to those illustrated for *Tristychius* by Dick (1978, fig. 9). *Antarctilamna*, *Xenacanthus*, *Tamiobatis*, and '*Cladodus*' *wildungensis* resemble each other in the relatively elongate otic region, a resemblance which has been interpreted as phylogenetically significant by Schaeffer and Williams (1977).

A few other canals and foramina have been noted in the material. ANU 35333 shows a trace of a narrow transverse canal (*tr.c*) passing behind the assumed buccohypophysial foramen. A swelling in this region connecting the paired longitudinal ridges suggests a median confluence of canals, perhaps to give an arrangement for the internal carotids like that figured by Schaeffer (1981, fig. 12). A fairly large ventral foramen in the base of the otic process may be for the vagus nerve (*10*, text-figs. 6A, 7), and surrounding cracks may be remnants of a ventral otic notch (cf. Schaeffer 1981, fig. 6). A canal on the broken posterior edge of ANU 35333 (*p.c*, text-fig. 6A) may have carried a spino-occipital nerve, or perhaps the occipital artery,



TEXT-FIG. 7. *Antarctilamna prisca* gen. et sp. nov. Partial reconstruction of the braincase in ventral view. Dashed lines on the right side indicate the probable extent of the precerebral fontanelle and left orbital cavity. A groove is restored for the left lateral dorsal aorta, as preserved in all available specimens, but this artery may have been contained in a canal in the braincase floor. Assumed course of major arteries indicated by dashed lines on the left side of the figure: *orb*, orbital cavity; *soc*, subocular shelf; for other abbreviations see text-fig. 6.

and two smaller canals (*10 st*) passing dorsally through the otic process are in the appropriate position for the supratemporal branch of the vagus nerve.

The material provides little information on the structure of the dorsal surface of the braincase. As noted above, the extent of the precerebral fontanelle is well shown (text-fig. 6), whilst the anterior extremity of the left orbital cavity is partly indicated as an impression in CPC 16994. The probable configuration of these structures is shown by dashed lines in text-fig. 7 (right side). A final point is that the extensive subocular shelf indicated in ventral view for *Antarctilamna* suggests an interorbital region which was narrower dorsally than ventrally, as in *Tristychius* (see Dick 1978, fig. 9), and unlike *Xenacanthus*, *Tamiobatis*, and '*Cladodus*' as figured by Schaeffer (1981).

Jaws and visceral arches. Apart from the traces of ceratobranchials in CPC 21187 (text-fig. 2), no other remains of jaws or visceral arches have been identified in the Antarctic material. In the Bunga collection, however, there are impressions of various shapes and sizes which lack dermal ornament, and therefore may be elasmobranch remains. Many are fragmentary, and no positive branchial arch elements have been identified, but two specimens are tentatively determined as remains of the palatoquadrate. CPC 21212, preserved in part and counterpart, provides information on the morphology of the postorbital ramus and mandibular joint (text-fig. 8A, B, D; Pl. 88, figs. 2, 3), although the suborbital ramus is unfortunately missing. The configuration of the ventral margin on the preserved portion, concave posteriorly with a blunt protuberance (*v.pr*) towards the palatine region, corresponds well with the form of the palatoquadrate in *Xenacanthus* (Hotton 1952, pl. 58). The second specimen (CPC 21213) is less clearly preserved, being intimately associated with other undeterminable remains (possibly elasmobranch), and also badly fractured. As interpreted here (text-fig. 8C) it shows a fairly long postorbital, and short suborbital ramus, in total proportions being more elongate than previously figured xenacanth palatoquadrates (e.g. Hotton 1952; Moy-Thomas and Miles 1971, fig. 9.12). Better preservation is required for these apparent differences in palatoquadrate shape to be assessed properly, and for the present both examples are assumed to be conspecific with the other elasmobranch material from this locality.

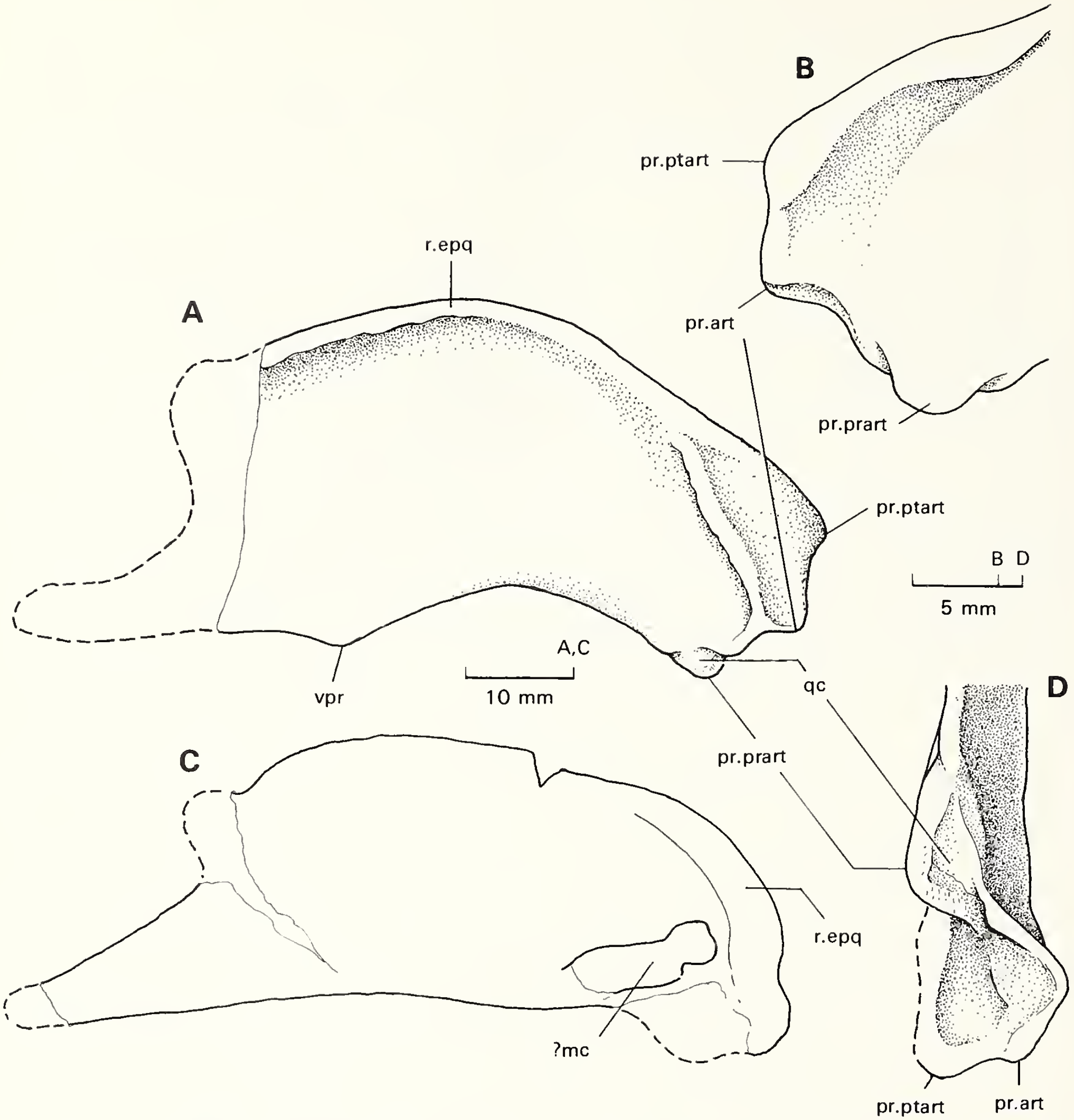
In both specimens the quadrate part of the cartilage is heavily developed, with a strong extra-palatoquadrate ridge (*r.epq*). In CPC 21212 this ridge is carried posteriorly on a rounded expansion, which in mesial view (Pl. 88, fig. 3) is seen to form a distinct concavity just above the mandibular joint. This concavity may have carried the hyomandibula, which is reconstructed by Hotton (1952, fig. 1) in a corresponding position for *Xenacanthus*. Alternatively, it may have been the insertion area for ligaments binding the mandibular joint. There is a similar groove for the hyomandibula on the palatoquadrate of acanthodians, but it is more dorsal in position (e.g. Miles 1973, fig. 12). As previously noted by Hotton (1952), the dental furrow in these specimens lacks the series of shallow vertical grooves seen in '*C.*' *wildungensis*.

A good idea of the structure of the mandibular joint is provided by CPC 21212. A projection on the ventral margin (*pr.prart*, text-fig. 8A) carries a depression on its lateral surface (*qc*), which may correspond to the 'quadrate concavity' described for *Xenacanthus* by Hotton (1952, pl. 58). This must have formed the anterior part of the double mandibular joint, by receiving a dorsal process from Meckel's cartilage. The ventral projection has much the same position as the prearticular process of the palatoquadrate in *Acanthodes bronni* (see Miles 1973, fig. 12), although other elasmobranchs with the double joint apparently lack this process (e.g. Allis 1923, fig. 29; Gross 1938, figs. 1, 3; Hotton 1952, fig. 1). The main articular process of the palatoquadrate (*pr.art*) is less pronounced in *Antarctilamna* than in the other forms just cited, and a postarticular process is visible in mesial view (*pr.ptart*), again as in acanthodians (Miles 1973, fig. 12B). A ventral view of the articular region emphasizes the close similarity to acanthodians in the arrangement of these three processes and associated articular surfaces (compare text-fig. 8D, and Miles 1973, fig. 13B). Particularly noteworthy is the position of the anterior articular depression (*qc*) on the lateral face of the prearticular process, as Miles has described. By contrast, this articulation in other elasmobranchs (Allis 1923; Gross 1938; Hotton 1952) lies on the mesial face of the palatoquadrate. Since the palatoquadrate of *Antarctilamna* is probably the oldest known example of this element in elasmobranchs, such a resemblance could be regarded as having phylogenetic significance (see Jarvik 1977; cf. Miles 1973, p. 72). This is considered further below. The corresponding region in CPC 21213 is obscured by a superimposed impression, possibly the posterior end of Meckel's cartilage (*?mc*, text-fig. 8B).

Genus XENACANTHUS Beyrich
Xenacanthus sp.

Plate 89, figs. 1–4; text-fig. 3E–G

1972 'tooth (which)... resembles the diplodont... teeth found in *Xenacanthus*'; Ritchie *in* McKelvey *et al.*, p. 351.



TEXT-FIG. 8. *Antarctilamna prisca* gen. et sp. nov. A, lateral view of left palatoquadrate, CPC 21212 (cf. Pl. 88, fig. 2). B, D, mesial and ventral views of the articular region of the palatoquadrate showing the mandibular joint, after CPC 21212. C, lateral view of possible left palatoquadrate, CPC 21213. ?*mc*, superimposed impression, possibly part of Meckel's cartilage; *pr.art*, articular process; *pr.prart*, prearticular process; *pr.ptart*, postarticular process; *qc*, quadrate concavity; *r.epq*, extra-palatoquadrate ridge; *v.pr*, ventral protuberance.

Material. Eighteen isolated teeth from Portal Mountain (CPC 21214–21217; AMF 54329–54331, 55573), and one (CPC 21228) from near Mt. Ritchie, south Victoria Land, Antarctica.

Remarks. These teeth may be distinguished from the smaller diplodont teeth described above on the following characters: the equal size of cusps, their curvature in different planes, and in a labial rather than a lingual direction, the absence of central cuspules, and the deeper, more bulbous base. There are no large ctenacanthiform spines at the Portal locality, where most of these teeth were found, and it is assumed for the present that two genera with diplodont teeth were represented in the Antarctic fauna. By their combination of characters these teeth may also be distinguished from previously described species of *Xenacanthus*, but in the absence of other remains (e.g. barbed cephalic spines) they are left for the present in open nomenclature.

Description. These teeth are known only from Portal (two horizons) and near Mt. Ritchie (Section A5). They are most common from the lower horizon in the Portal section, from where they were first recognized by Ritchie (in McKelvey *et al.* 1972). They differ in several respects from the teeth in CPC 21187. They are larger (between 3·5 and 8·0 mm across the base), the height of the biggest example (CPC 21218) being estimated at 11 mm. In addition the base is noticeably more extensive and bulbous relative to the length of cusps, the cusps are less slender and slightly shorter, and instead of being of similar proportion one cusp is considerably longer and larger than the other. However, according to Hotton (1952, p. 496) at least two of these features (proportionately larger base and less slender cusps) may vary with size within a species.

Each cusp is rounded in section distally, but proximally the (assumed) lingual face is flattened, and separated from the more rounded side of the cusp by a fine ridge continuous between cusps (*ri*, text-fig. 3F). This probably formed a cutting edge, as in the teeth of *Antarctilamna* described above. In two examples with the surface of the cusps well preserved, the flattened side is smooth (Pl. 89, fig. 1) but the opposite side carries several vertical striations (Pl. 89, fig. 4). By comparison with *Antarctilamna* it may be assumed for the purpose of description that the smooth side is lingual and the striated side labial. Thus oriented, however, the teeth differ from those of *Antarctilamna* in that the cusps apparently curve towards the opposite (labial) side (Pl. 89, fig. 2; cf. text-fig. 3D). In addition, each cusp is curved in a slightly different plane, giving them a twisted appearance in dorsal view (Pl. 89, fig. 3). As first noted by Ritchie (*in* McKelvey *et al.* 1972), there is consistently no small middle cuspule in these teeth, although this is reported to be variable in other species (e.g. *X. texensis* and *X. compressus*; see Hotton 1952, p. 497). The morphology of the base in both lingual and labial views is well shown in two specimens. CPC 21219 and several other specimens exhibit a notch in the basal margin (text-fig. 3E, F) similar to that figured by Hotton (1952, fig. 2B) for *X. depressus*. This expanded side of the base is assumed for the purpose of description to correspond to the lingual torus of other forms, although in an antero-posterior view (Pl. 89, fig. 2) the cusps are not clearly situated closer to the labial margin (cf. Hotton 1952, p. 495 n.). In CPC 21215 there is a large pore above the notch corresponding to the similar pore on the lingual torus in *Antarctilamna*. On the (assumed) labial side the basal margin is concave (Pl. 89, fig. 4), with no sign of the basal tubercle figured by Hotton (1952). Nor is there any sign of an apical button on the lingual torus.

Genus MCMURDODUS White

Mcmurdodus? cf. *featherensis* White

Plate 88, fig. 4; text-fig. 3H

Material. One tooth (CPC 21229) from Mt. Ritchie, south Victoria Land, Antarctica.

Remarks. This tooth is twice the size of the holotype of *M. featherensis*, and is generally dissimilar (White 1968, fig. 1; pl. 1, fig. 6). However, both teeth are of elongate compressed form, with the larger lateral cusps separated by a long cutting edge, and minor cusps at one or both ends of the tooth. The main difference is the almost horizontal direction of the cusps in White's specimen, and its thin root, but the latter feature may be an artefact since the exposed root surface is abraded. White tentatively referred his tooth to the notidanoids, which are otherwise unknown in Palaeozoic rocks (although an early differentiation of this group has been suggested; see Patterson *in* Andrews *et al.* 1967). However, the tooth referred here to the genus shows no resemblance to other hexanthid teeth, so one or other assignment is probably incorrect. It may be significant that both teeth come from near the top of the Aztec Siltstone, and for the purpose of description this tooth is tentatively compared with the type species of *Mcmurdodus* on the basis of the resemblances listed above.

Description. CPC 21229 is 10 mm across the base, which is partly broken away but preserved as a clear impression. The smaller of the two main cusps is incomplete and its original size and shape uncertain. Noteworthy features of the tooth are the wide separation of the major cusps, the prominent striations, the development of a serrated irregular cutting-edge between the lateral cusps, and the minor cusp developed at one end (right side of text-fig. 3H).

DISCUSSION

This new material shows that several elasmobranchs were established in freshwater environments of East Gondwana towards the end of Middle Devonian time, and at least one of these (*Antarctilamna prisca*) possessed both diplodont teeth and ornamented dorsal fin-spines. Teeth of this type are characteristic of the xenacanth sharks, which are well known especially from Carboniferous and Permian freshwater deposits, but do not bear fin-spines. It has been suggested, however (e.g. Glikman 1964; Schaeffer and Williams 1977), that the characteristic cephalic spine of xenacanthids may be a modified and transposed fin-spine, and this would appear to be confirmed by this new material. I suggest that *Antarctilamna* is immediately related to *Xenacanthus*, on the basis that diplodont teeth are a synapomorphy, and that dorsal fin-spines are plesiomorphic. The proper assignment of the other teeth referred above to the genus *Xenacanthus* will depend on the discovery of associated material exhibiting other specializations of the genus (e.g. a cephalic spine, biserial pectoral fins, diphycercal tail, elongate dorsal and double anal fins, etc.).

Fin-spines also occur in several other groups of early elasmobranchs, and they have variously been regarded as a primitive feature for the whole group (e.g. Patterson 1965, p. 197; Schaeffer 1967, p. 13), for chondrichthyans generally, or possibly for all gnathostomes except placoderms (Schaeffer and Williams 1977, p. 294). Patterson (1965) commented that the spines of elasmobranchs and holocephalans are similar structures which have arisen and evolved in the same way, whilst Schaeffer and Williams (1977) have implied that the primitive condition for both holocephalans and elasmobranchs was probably a single spinose dorsal fin (cf. Patterson 1965, p. 197). However, most early elasmobranchs known to have a single dorsal fin lack fin-spines, and those with fin-spines, where known, generally have two spinose dorsal fins. The relevance to this problem of the new information provided by *Antarctilamna* can only be considered within the context of a hypothesis of its relationships to other early elasmobranchs.

As just noted, the teeth of *Antarctilamna* may be taken to indicate an immediate relationship to *Xenacanthus*. However, the origin and relationships of the xenacanthids themselves are obscure, and under the grade concept of elasmobranch evolution elaborated by Schaeffer (1967; also Zangerl 1973) they have been regarded as a highly specialized offshoot of the basal elasmobranch stock. Because of their poor fossil record (mainly isolated teeth and spines), the early history of elasmobranchs generally has been viewed only in terms of evolutionary grade. Recently, however, attempts have been made to move towards a more phylogenetic approach to their early diversification. Maisey (1975, p. 558) suggested that 'phalacanthous sharks belong to a single phyletic unit within the elasmobranchs', and he proposed a subdivision of this unit into three groups (Euselachiformes, Hybodontiformes, and Ctenacanthiformes). He further argued (Maisey 1975, 1977, 1978; cf. Schaeffer 1967; Moy-Thomas and Miles 1971), mainly on the basis of fin-spine structure, that the euselachians are more closely related to ctenacanthiform than to hybodont sharks (see also Schaeffer and Williams 1977). This has since been challenged by Dick (1978, p. 107), on the grounds that resemblances in fin-spine structure are no more than shared primitive features. A more explicit

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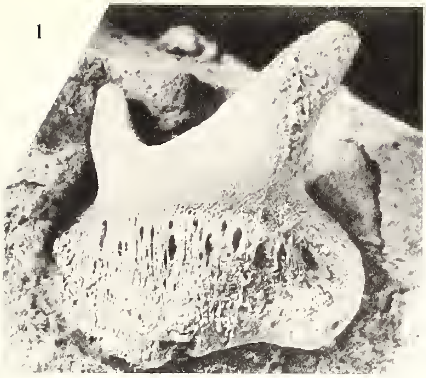
EXPLANATION OF PLATE 89

Figs. 1–4. *Xenacanthus* sp. 1, 2, 3, isolated tooth (CPC 21219) in (assumed) lingual, antero-posterior and dorsal views (latex rubber cast), × 6. 4, isolated tooth (CPC 21218) in (assumed) labial view (latex rubber cast), × 6; all from Aztec Siltstone, Portal Mountain, south Victoria Land, Antarctica.

Figs. 5–8. *Antarctilamna prisca* gen. et sp. nov. 5, endocranial cast (CPC 21211) in ventral view, × 2. 6, portion of shagreen from piece *j* of the holotype (CPC 21187). Abraded scales are shown in the lower right corner; in the upper left corner scale crowns have broken off, to show impressions of the cup-shaped scale bases, × 16. 7, tooth in labial view from piece *a* of the holotype (CPC 21187), × 12. 8, isolated tooth (CPC 21198) in labial view (latex rubber cast), × 12. Figs. 5, 8 from Bunga Beds, Bunga Beach, south coast of New South Wales. Figs. 6, 7 from Aztec Siltstone, Lashly Mountains, south Victoria Land, Antarctica.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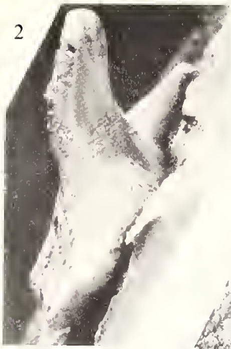
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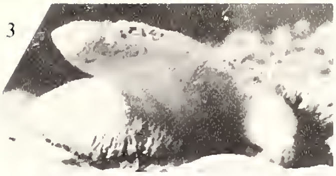
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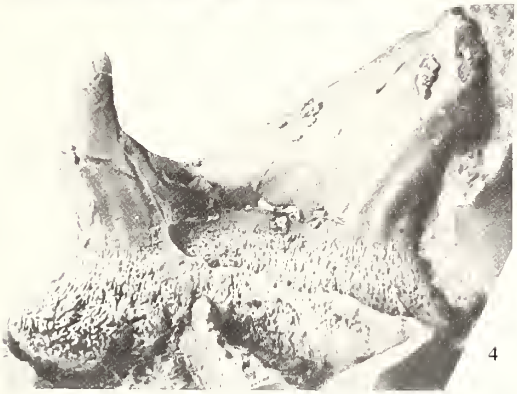
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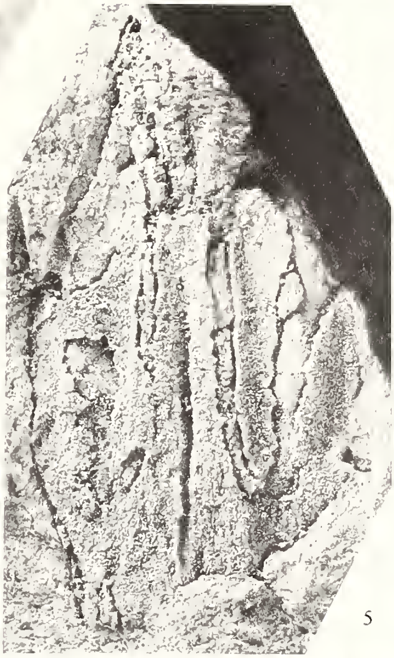
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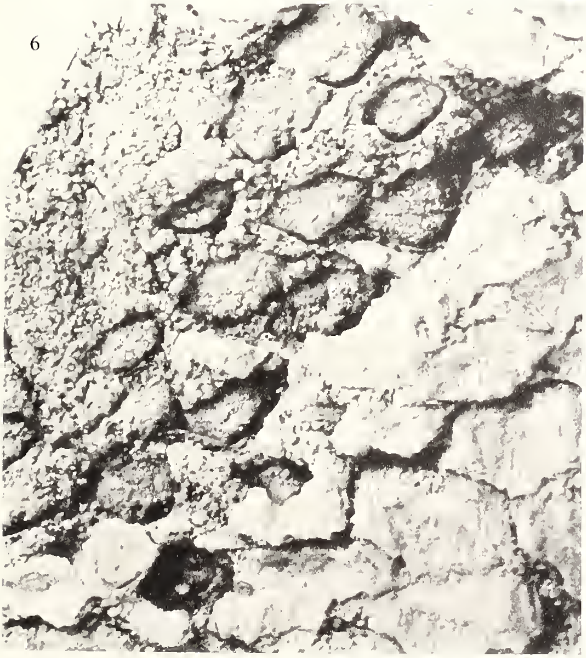
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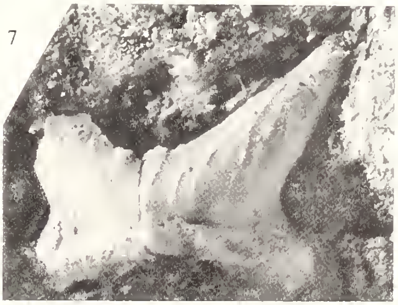
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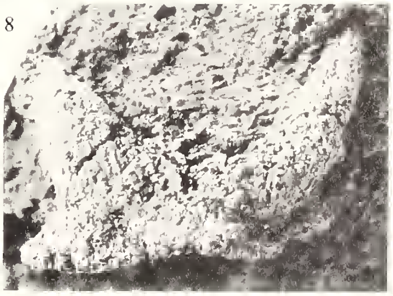

8

YOUNG, *Xenacanthus* and *Antarctilamna* scheme of relationships for early elasmobranchs in the form of a cladogram was presented by Schaeffer and Williams (1977). They regarded xenacanthids (as represented by the genus *Xenacanthus*) to be the pleisomorph sister-group of other representative genera of early elasmobranchs (*Denaea*, *Cladoselache*, *Hybodus*, *Ctenacanthus*, *Palaeospinax*), which they united on the basis that the triangular basal portion of the pectoral fin is a derived feature. Schaeffer and Williams also followed Maisey in placing *Ctenacanthus* in closer relationship to *Palaeospinax* than is *Hybodus* (but cf. Schaeffer 1981).

Schaeffer and Williams (1977) acknowledged that their preliminary scheme of relationships would be subject to testing and emendment as new information became available, and on the new evidence of *Antarctilamna* an alternative scheme can be proposed. [Schaeffer (1981) has also put forward a modified scheme of relationships for some of the genera considered below, based mainly on braincase structure. This has not been considered in detail, but is generally compatible with conclusions reached here using other characters.] As previously noted, the fin-spine morphology of *Antarctilamna* is ctenacanthiform according to Maisey's criteria (see above), and using Schaeffer and Williams's (1977) cladogram, but with *Antarctilamna* and *Xenacanthus* as sister-groups, these resemblances would have to be independently acquired. Alternatively, one may accept Dick's (1978) arguments that the fin-spine resemblances between ctenacanths and euselachians are symplesiomorphies, and that the latter are more closely related to hybodonts, which has long been the traditional view. The two alternative schemes of interrelationship, incorporating the new evidence of *Antarctilamna*, are given in cladogram form in text-fig. 9. The following may be listed as unparsimonious consequences of Schaeffer and Williams's (1977) scheme (letters refer to text-fig. 9A):

(*a*) Independent acquisition of the ctenacanthiform type of fin-spine and teeth with an expanded lingual torus (Maisey 1975) in *Antarctilamna* and the common ancestor of *Ctenacanthus* and *Palaeospinax*.

(*b*) Independent loss of the metapterygial axis of the pectoral fin in *Hybodus* and *Palaeospinax*.

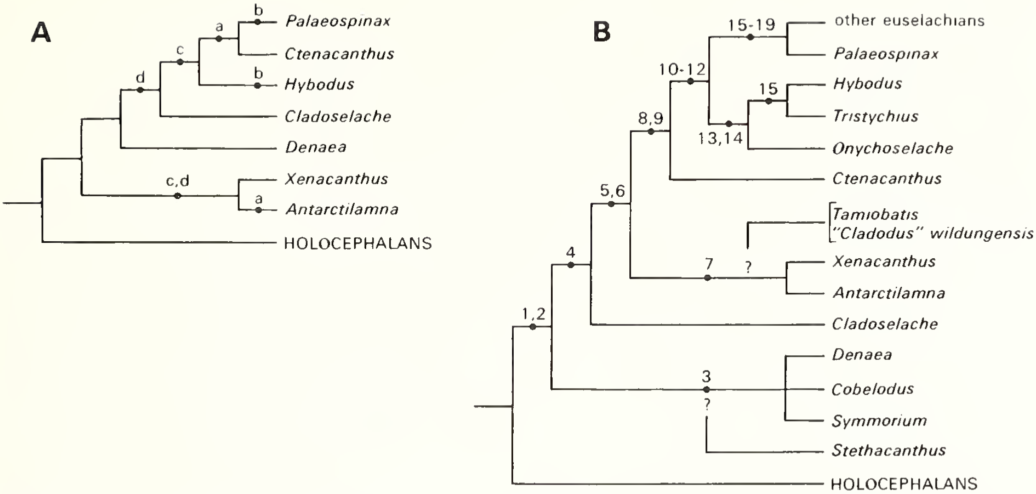
(*c*) Independent acquisition of an anal fin in *Xenacanthus* and the common ancestor of *Hybodus*, *Ctenacanthus*, and *Palaeospinax* (but Schaeffer and Williams 1977 suggest that its double structure in xenacanthids indicates separate derivation).

(*d*) Independent closure of the hyoidean gill slit in xenacanthids and the common ancestors of *Cladoselache*, *Hybodus*, *Ctenacanthus*, and *Palaeospinax* (assuming the condition described for *Cobelodus* is primitive; see below).

Unique specializations (autapomorphies) of the taxa shown on this cladogram are listed by Schaeffer and Williams (1977). They apparently regard the postaxial radials in the pectoral fin of *Xenacanthus* as a specialized feature, but this raises a difficulty because they elsewhere propose the long pectoral metapterygial axis as an elasmobranch autapomorphy, with this axis presumably lacking postaxial radials. It is thus not clear in what respect the pectoral fin shape given as a synapomorphy of all taxa above *Xenacanthus* in their cladogram differs significantly from the postulated primitive condition of the fin, and some other character is needed to unite these forms.

Under the new scheme of relationships proposed here (text-fig. 9B) these unparsimonious consequences are eliminated. It will be noted that this also applies to the cladogram based on braincase structure proposed by Schaeffer (1981), which, except in its treatment of '*Ctenacanthus*', generally conforms to that put forward here. Further to Schaeffer's new scheme, the genera *Tristychius*, *Onychoselache*, and *Cobelodus* have been included here on the basis of recent detailed description (Zangerl and Case 1976; Dick 1978; Dick and Maisey 1980). In addition, *Cobelodus*, *Symmorium*, and possibly *Stethacanthus* are shown as closely related to *Denaea* (Zangerl 1973; Schaeffer and Williams 1977), and *Tamiobatis* and '*Cladodus*' *wildungensis* are tentatively grouped with xenacanthids, on the assumption that the long otic region of the braincase is specialized. The synapomorphies supporting the scheme of relationships put forward here are as follows (numbers refer to text-fig. 9B):

1. Prominent metapterygial axis in the pectoral fin; palatoquadrates with palatine processes and symphysial connection.
2. Loss of pharyngohyal, and development of an articulation between the hyomandibula and the braincase (assuming the unmodified hyoid arch of holocephalans is primitive).



TEXT-FIG. 9. A, cladogram of elasmobranch interrelationships proposed by Schaeffer and Williams (1977), but with *Antarctilamna* included as the sister group of *Xenacanthus*. B, alternative scheme of interrelationships for certain elasmobranchs. For explanation of letters and numbers see text.

3. Loss of dorsal fin-spine, and development of a short deep neurocranium, and large orbits.
4. Two dorsal fins, each with an unornamented spine lacking an outer orthodentine coat.
5. Ctenacanthiform type of fin-spine, consisting mainly of osteodentine with little or no lamellar tissue, and an ornamented outer coat of orthodentine. Spine cross-section is triangular with a posteriorly placed central cavity, a thinner, flat-to-concave posterior wall, and no posterior ornament or denticles.
6. Evolution of an anal fin.
7. Braincase with elongated otic region, and large semicircular canals.
8. Fin-spines deeply embedded between the myotomes.
9. Tribasal pectoral fin.
10. Caudal fin not lunate.
11. Calcified ribs.
12. Pectoral metapterygial axis reduced or lost.
13. Hybodontiform type of fin-spine, oval in cross-section, with a centrally placed cavity and posterior denticle rows.
14. Teeth lacking a lingual torus.
15. Aplesodic pectoral fin.
16. Calcified centra.
17. Jaws sub-terminal and hyostylic.
18. Right and left halves of pectoral and pelvic girdles fused ventrally.
19. Smooth fin-spines, with clearly defined mantle and trunk components, the latter made up largely or completely of lamellar tissue.

Some remarks are required to elaborate on this list of characters. As noted by Schaeffer and Williams (1977), unique derived characters for the elasmobranchs as a whole are difficult to find, and the pectoral metapterygial axis is at present the only one they mention which has not been disputed. Miles (1973, p. 71) has suggested, however, that the symphysial connection between palatoquadrates, and their palatine processes, may also be elasmobranch specializations. With regard to character 2, the presence of an unmodified hyoid arch in ancestral elasmobranchs is implied both by the putative pharyngohyal in holocephalans, and by the different relationship of the hyomandibula to the lateral head vein and hyomandibular nerve in modern elasmobranchs and osteichthyans. However, both points are of disputed significance (e.g. Patterson 1965, p. 103 n.; Gardiner 1973, p. 109). Furthermore, Zangerl and Williams (1975) have suggested that in *Cobelodus* the hyoid gill-slit was still complete, even though the epihyal had developed an articulation with the braincase. Thus, it can be hypothesized on this evidence that all elasmobranchs lack a pharyngohyal, but whether this is a primitive gnathostome character, or an independently acquired specialization in elasmobranchs (or elasmobranchs plus another gnathostome group), is an unresolved question (see also Stahl 1980). Character 3 as used above was similarly treated by Schaeffer and Williams (1977), although Maisey (1975) previously suggested that the spine(s) of *Cladoselache* were acquired independently of other spinose forms (see also Zangerl 1973). The absence of a deeply inserted portion is here interpreted as a primitive feature shared with *Antarctilamna*, which, like *Cladoselache*, is assumed to have two dorsal fins and spines, although the evidence is not conclusive. As noted above, typical phalacanthous sharks have two dorsal fin-spines, although comparison with holocephalans suggests that a single spinose dorsal fin might be the primitive elasmobranch condition. Of relevance here is the inadequately known *Stethacanthus*, which is reported to have a single unornamented dorsal spine (Zangerl 1973; Lund 1974), and is tentatively suggested by Schaeffer and Williams (1977, p. 299) to be a sister taxon to the *Denaea* complex. If confirmed, this would indicate that the absence of a dorsal spine in *Denaea* and its close relatives is secondary, and would obviate the difficulty otherwise implied by the cladogram of text-fig. 9B, that the dorsal spines of elasmobranchs and holocephalans were independently acquired. The tribasal pectoral fin is shown as present in *Ctenacanthus* (character 9), although this is not so in Maisey's reconstruction (1975, fig. 5; cf. Zangerl 1973, p. 9). Finally, two anomalies are raised by the recent paper of Dick and Maisey (1980). First, they suggest (p. 372) that the reduced postorbital part of the palatoquadrate is a shared derived character of *Onychoselache*, *Tristychius*, Mesozoic hybodontids, *Palaeospinax*, and other neoselachians, but some Recent forms (e.g. Compagno 1977, fig. 2) show this to be invalid. Secondly, they describe the pectoral fins of *Onychoselache* as plesodic. But if the previous suggestion of Dick (1978, p. 107) is accepted, that the similar fin-spine of ctenacanths and early euselachians is a symplesiomorphy, it follows that the hybodontiform spine morphology must be specialized. This is unsatisfactory as it implies (text-fig. 9B) that the aplesodic fin must have evolved independently in the common ancestor of *Tristychius* and *Hybodus*, and in the common ancestor of *Palaeospinax* and higher euselachians. Using a similar type of argument, it is clear that the close resemblance mentioned above in the structure of the mandibular joint between *Antarctilamna* and acanthodians cannot be regarded as phylogenetically significant, since under either hypothesis of relationships this must have been acquired independently in the two groups.

Notwithstanding the above anomalies, and conditional upon confirmation that *Stethacanthus* both retains a single spinose dorsal fin and exhibits synapomorphies with *Denaea* and *Cobelodus*, I suggest that the cladogram of text-fig. 9B depicts a more parsimonious interpretation of early elasmobranch interrelationships than has previously been put forward. This interpretation incorporates the new information provided by *Antarctilamna*, and it implies that one of the three orders proposed by Maisey (1975), the Ctenacanthiformes, is paraphyletic. On the other hand, a close hybodontid/euselachian relationship is supported, and, as noted by Dick (1978), this suggests that euselachians had already differentiated by early Carboniferous time.

To conclude this discussion a brief comment should be made concerning some biogeographic aspects of the new elasmobranch occurrences dealt with here. There have recently been suggestions that early tetrapods (Panchen 1977; Janvier 1978*b*), and certain osteolepid fishes (Janvier, Termier and Termier 1979) and placoderms (Young 1981) had a Gondwanan origin. The new elasmobranch occurrences described here might indicate that xenacanths can be added to this list. There is little doubt that both the Bunga Beds and Aztec Siltstone sediments are non-marine, this being consistent with the accepted habitat of xenacanths, which are widely known from Carboniferous and Permian freshwater deposits. It could be suggested, therefore, that their early dispersal was limited by marine barriers, and that changed continental configuration permitted their geographic expansion during the Carboniferous and Permian. But the early North American occurrences of isolated diplodont teeth are in marine deposits, as are some of the elasmobranch remains from Iran and South America (Janvier 1978*a*, 1980), so such a simple hypothesis regarding their distributional history is unsatisfactory. Nevertheless, the Antarctic and south-east Australian occurrences, considered with reported 'ctenacanth' spines from several different localities and horizons in Iran, and other elasmobranch remains from South America (otherwise devoid of authenticated Devonian fish occurrences), certainly suggest that an important part of early elasmobranch evolution took place on the Gondwana continents. This has potential biogeographic significance, and when these new faunas have been studied in more detail they are likely to further modify current ideas regarding the early differentiation of major elasmobranch taxa. Such ideas have previously been based almost entirely on Northern Hemisphere occurrences.

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CONODONTS FROM THE UPPER PERMIAN STRATA OF NOTTINGHAMSHIRE AND NORTH YORKSHIRE

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ABSTRACT. Conodont elements have been found in samples of Upper Permian age from three separate areas in Nottinghamshire and North Yorkshire. The collections from Nottinghamshire comprise specimens derived from older rocks; in one area the source was of Carboniferous age, in the other it was Devonian. Collections from North Yorkshire appear to be largely indigenous and contain the zonal conodont *Merrillina divergens* (Bender and Stoppel) and elements of *Ellisonia*. These are the first identifiable Permian conodonts recorded from Britain.

CONODONTS from the British Permian are almost unknown. The only published record is of a single indeterminate fragment from the lower subdivision of the Lower Magnesian Limestone (Zechstein 1) of the Aiskew Bank Farm borehole, North Yorkshire (Pattison 1978, p. 5, fig. 6). Conodonts have been reported from other Zechstein 1 deposits of Germany by Bischoff and Ziegler (1957), Malzahn (1957), and Seidel (1959), but not until the landmark paper of Bender and Stoppel (1965) were German Zechstein 1 conodonts described systematically. Jordan (1969) also contributed a short paper on German Zechstein 1 conodonts, and Szaniawski (1969) recorded the first Zechstein 1 conodonts from Poland, but knowledge of north-west European Upper Permian faunas is still limited. Elsewhere, recent research has greatly increased the information available on Upper Permian conodonts. Much of this literature has originated from North America, where Sweet (i.a. 1970*a*, *b*, 1973, 1976), Clark and Behnken (1971), Behnken (1975), and Wardlaw and Collinson (1979*a*, *b*) have all made significant contributions. In Europe a large number of papers have been published by Kozur (e.g. 1975, 1977, 1978), alone or with co-authors, that cover a wide range of Permian and Triassic morphological and biostratigraphical topics.

In this report we record the first identifiable conodonts from British Permian strata. All our samples are from the first transgressive phase of the Zechstein Sea (Zechstein 1), represented by the Lower Magnesian Limestone and the Permian Lower Marl. Our stratigraphical nomenclature follows Smith *et al.* (1974).

SAMPLE LOCALITIES

Locality numbering follows the system employed in the Micropalaeontology Unit, Geology Department, Nottingham University. The distribution of localities is shown in text-fig. 1, and the microfossil assemblages recovered by acetic acid digestion are listed in Table 1.

North Yorkshire

Loc. 283. Lower Magnesian Limestone. The Aiskew Bank Farm borehole drilled by the Institute of Geological Sciences, 800 m north of Bedale centre (Pattison 1978); SE 2667 8888. Five samples of grey-brown, fine-grained dolomite from the following depth intervals: 69–74 m, 74–79 m (both from upper subdivision), and 79–84 m, 84–89 m, 89.0–92.2 m (all from lower subdivision). The base of the Permian was encountered at 96.45 m.

Loc. 284. Lower Magnesian Limestone. The Sand Hutton borehole drilled by the National Coal Board, 3 km west of Thirsk station; SE 3789 8157. Five samples of grey-brown, fine-grained dolomite from the

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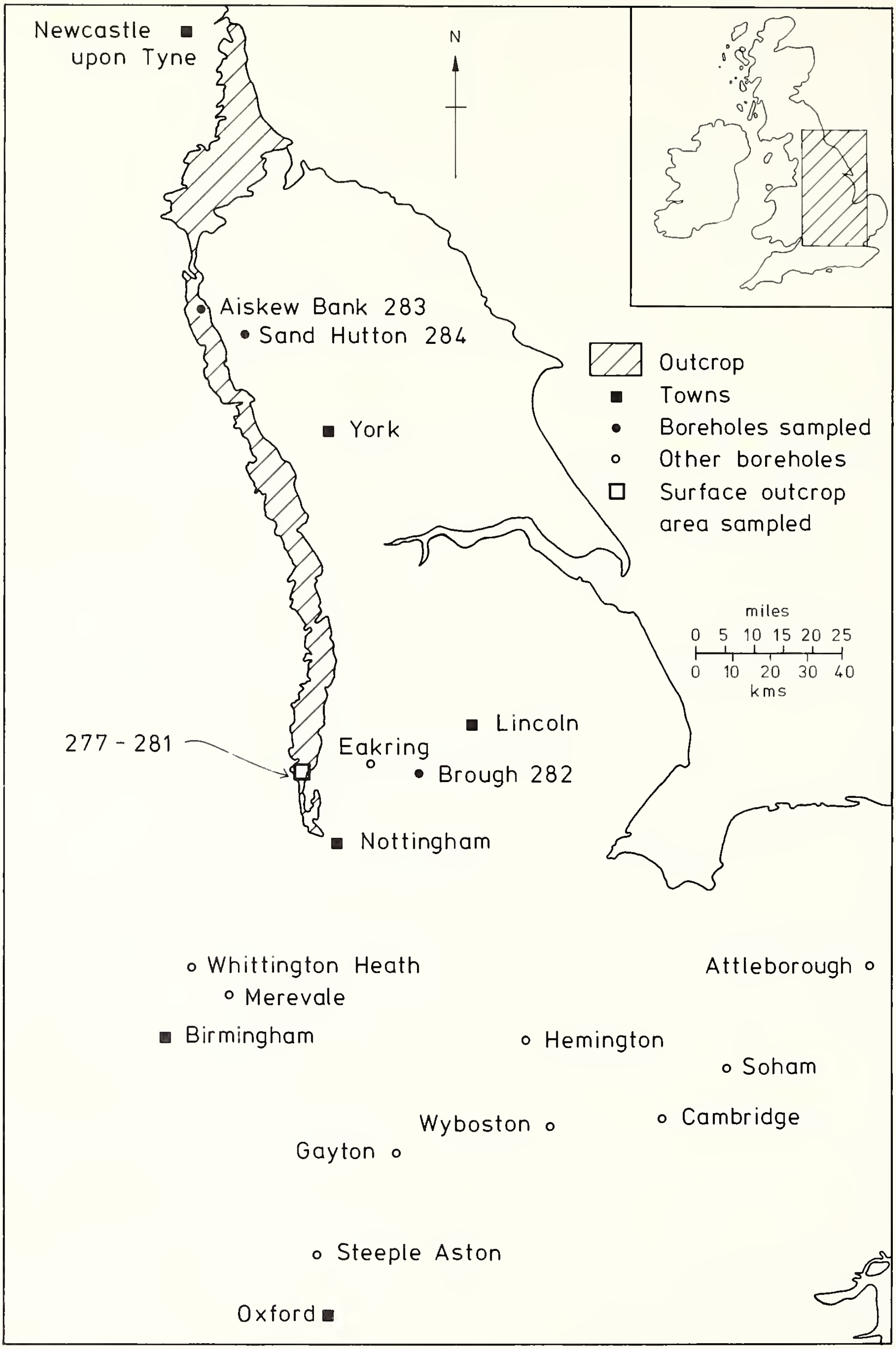

TEXT-FIG. 1. Upper Permian surface and borehole sample localities. Other boreholes are shown that penetrated Devonian strata. The outcrop of Magnesian Limestone and Permian mudstones is shown (after Geological Map of the U.K., 3rd edition 1979, Institute of Geological Sciences).

following depth intervals: 349.5–354.6 m, 355.8–367.9 m, 364.0–369.0 m, 381.75–384.75 m, and 385.0–386.64 m. The base of the Permian was encountered at 386.67 m.

Nottinghamshire

Loc. 277. Lower Magnesian Limestone. Abandoned railway cutting immediately west of Studfold (Smith, Rhys and Eden 1967); SK 499 556. Six samples of red, shelly, crystalline limestone.

Loc. 278. Permian Lower Marl. Road cutting in Teversal, immediately east of the railway bridge on the road to Fackley (Smith, Rhys and Eden 1967); SK 480 618. Five samples of very shelly, thin-bedded limestone.

Loc. 279. Lower Magnesian Limestone. Small excavation behind houses in Stony Houghton; SK 4925 6623. Five samples of grey and red carbonate, possibly dedolomite.

Loc. 280. Lower Magnesian Limestone. Railway cutting 450 m east of Teversal Colliery, at milepost 142; SK 4792 6204. One sample of blue-hearted, brown dolomite.

Loc. 281. Lower Magnesian Limestone. Hillside exposure on Herrod's Hill, 375 m north of Huthwaite Market Place; SK 4680 6015. One sample of yellow dolomite.

Loc. 282. Permian Lower Marl. The Brough borehole, drilled by the National Coal Board in 1980 near Collingham, 325 m south-south-west of Glebe Farm; SK 8335 5840. One sample from a depth of 557 m of medium-grained, poorly calcareous sandstone.

SAMPLE NUMBER	WEIGHT (g)	CONODONTS	OTHER MICROFAUNA				
			F	O	H.S.	F.M.	S
277/1	1890	23	×			×	
-/2	2035	36				×	
-/3	1814	10				×	
-/4	1510	19	×			×	
-/5	1644	6			×	×	
-/6	1964	4	×			×	
278/1	2000	1	×		×	×	
-/2	1990	0	×		×	×	
-/3	2000	0	×			×	
-/4	1500	0	×			×	
-/5	1519	13	×			×	
279/1	2300	2	×			×	
-/2	2000	1	×				
-/3	1590	0					
-/4	2100	1				×	
-/5	1663	11				×	
280/1	1757	0	×				
281/1	1853	0	×			×	
282/1	2240	90	×			×	
283/1	3413	35	×		×	×	
-/2	2000	5	×		×	×	
-/3	2000	4	×		×	×	×
-/4	1900	31	×	×	×	×	
-/5	2000	2	×		×	×	
284/1	2000	3			×		
-/2	1654	4	×		×	×	×
-/3	1227	3	×		×	×	×
-/4	1531	0	×		×	×	
-/5	1744	0	×	×	×	×	

TABLE 1. Sample weights, conodont numbers, and distribution of other microfossils. F = foraminifera; O = ostracods; H.S. = holothurian sclerites; F.M. = fish microdebris; S = scolecodonts.

THE CONODONT ASSEMBLAGES AND THEIR SIGNIFICANCE

North Yorkshire, localities 283 and 284

The majority of the conodonts recovered from the North Yorkshire boreholes are demonstrably of Permian age, and our collections compare most closely with the faunas reported from Zechstein 1 deposits of north-west Europe.

A few elements in our material also resemble forms reported from Kashmir, Pakistan, and Greenland (Sweet 1970*a*, *b*, 1976), and North America. Diversity and numbers are low; most of the elements can be referred to apparatuses assigned to the genus *Ellisonia*. Identifications are given in Table 2.

Although we suspect the nature of the multi-element relationships of the majority of our specimens, our collections are too small to enable us to establish accurate apparatus reconstructions or to evaluate those proposed by other authors. Some specimens compare with described forms: for example, one Sc element (Pl. 90, figs. 5–7) is similar to the form named *Hindeodella triassica* by Müller (1956, p. 826, figs. 4, 5) and two of our M elements (Pl. 90, figs. 9, 14) may be close to *Lonchodina inflata* Bender and Stoppel (1965, p. 346, pl. 15, fig. 8) and *L. festiva* Bender and Stoppel (1965, p. 345, pl. 15, fig. 10) respectively. Our collections also contain probable

SAMPLE NUMBER / CONODONTS	LOC. 283					LOC. 284		
	1	2	3	4	5	1	2	3
Ellisonia cf E. triassica Prioniodinan element			1					1?
Ellisonia spp. Pb? elements	3							
M elements				5				
Sa elements	4							
Sa/Sb elements	1							
Sb elements	1							
Sc elements	3		1	4		1	1	
Fragments	12	1	1	11	1	1	3	
Merrillina divergens P element				4				
Indeterminate P element					1			
Gen. et sp. indet.	1	4	1	7		1		2

TABLE 2. Conodonts recovered from the North Yorkshire borehole samples. Samples 284/4 and 284/5 failed to yield conodonts. Multi-element notation follows Sweet and Schönlaub (1975).

representatives of two form-species erected by Szaniawski (1969); an Sa element (Pl. 90, fig. 8) compares with *Hibbardella baltica* Szaniawski (1969, p. 332, pl. 2, figs. 11, 12), and a Pb? element (Pl. 90, fig. 3) is similar to *Prioniodina lindstroemi* Szaniawski (1969, p. 332, pl. 2, figs. 6–9). A prioniodinan (Pb?) element included by Sweet (1970*a*, pl. 1, fig. 19) in multi-element *Ellisonia triassica* may also be represented (Pl. 90, fig. 4), but we do not have other robust elements with inverted cavities that are considered to be characteristic of this apparatus (Sweet 1970*b*, p. 235). However, many of our specimens could be accommodated in apparatuses of similar structure to those assigned to various species of *Ellisonia* (Sweet 1970*b*, pp. 224–239, pls. 4, 5). Some of the form-species present in our collections, first described by Bender and Stoppel (1965) and Szaniawski (1969), have been included in the multi-element genus *Stepanovites* by Kozur (1975, pp. 22–27), but we find it difficult to assess the relationships between this genus and *Ellisonia*, and, for the present, refer to our material under the older name.

Our collections also include a few specimens (Pl. 90, figs. 1, 2) of *Merrillina divergens* (Bender and Stoppel). In erecting the genus *Merrillina*, Kozur (1975, p. 21) noted that it was difficult to determine which ramiform elements were combined with the characteristic spathognathodontan elements; it seems likely that most of the elements here included in *Ellisonia* belong in the same apparatus as *Merrillina*. Solution of these taxonomic and nomenclatural problems awaits the study of large, well-preserved collections.

M. divergens has been reported from north-west European Zechstein 1 sediments (Bender and Stoppel 1965; Jordan 1969; Szaniawski 1969), and from the Upper Permian of North America (Clark and Behnken 1971; Behnken 1975; Wardlaw and Collinson 1979*a*, *b*). In America the species has proved to be of biostratigraphical value; Clark and Behnken (1971) recognized a '*Neospathodus divergens* Fauna' in the upper part of the Capitanian (upper Guadalupian) of Nevada, where Behnken (1975, p. 293) subsequently delimited a *Neogondolella rosenkrantzi–Neospathodus divergens* Assemblage zone with a base marked by the appearance of *N.* (= *Merrillina*) *divergens*. Wardlaw and Collinson (1979*b*) followed Clark and Behnken (1971) in recognizing a *M. divergens* Zone within the Guadalupian throughout the Great Basin and Rocky Mountain regions of the western United States. There is, however, some dispute as to whether the North American specimens are conspecific with *M. divergens*. Kozur and Mostler (1976, p. 11, pl. 1, fig. 8) refigured the specimen illustrated by Clark and Behnken (1971, pl. 2, fig. 6) as the holotype of new species, *M. praedivergens*, which they considered to be the stratigraphical antecedent of *M. divergens*. In his proposals for a new standard chronostratigraphy for the Permian System, Kozur (1977) placed the Capitanian stage at the top of the Middle Permian and (Kozur 1978) defined a '*Gondolella bitteri–Stepanovites meyeni–Merrillina praedivergens* Assemblage Zone' that spanned the stage. *M. divergens* was confined to his succeeding Abadehian Stage at the base of the Upper Permian, where a '*Gondolella bitteri–Stepanovites inflatus–Merrillina divergens* Assemblage Zone' could be recognized in Iran, Europe, and Greenland. We remain wary of accepting this biostratigraphic scheme until the faunal sequences have been demonstrated in a single area. Within the Zechstein area, however, our recovery of *M. divergens* corroborates the established correlation of the Lower Magnesian Limestone with the Zechsteinkalk (Smith *et al.* 1974).

Nottinghamshire localities 277–281

Conodonts were recovered from samples from localities 277, 278, and 279. Numbers are small and the specimens are mostly fragmentary, ranging from 0.125 mm to 0.35 mm in size. The majority are too broken to allow identification, but a few are sufficiently well preserved for generic, and in some cases possible specific, assignments to be suggested.

Most of the identifiable specimens compare closely with elements of known Carboniferous species. For example, one specimen of an M element (Pl. 91, fig. 5) is very similar to illustrated specimens of the form-species *Neoprioniodus singularis* (Hass), a common constituent of British Viséan and Namurian faunas (Rhodes, Austin and Druce 1969, p. 160; Higgins 1975, p. 68). The form *Metalonchodina bidentata* (Gunnell) is probably represented in our material by a single broken specimen (Pl. 91, fig. 1) with a prominent cusp, and large adjacent laterally compressed denticle diverging from it at an angle of 22°. Again, this is known from the British Viséan and Namurian, as is *Spathognathodus campbelli* Rexroad, with which we compare one Pa element (Pl. 91, fig. 2) on the basis of general morphological similarity and, particularly, the presence of a dark longitudinal stripe in the blade. Fragments of platform elements are rare in our collections, and only one allows a suggested identification. This specimen (Pl. 91, fig. 10) displays part of the blade and inner lateral parapet of a dextral element comparable with specimens referred to the Carboniferous genus *Cavusgnathus*. Specific assignment is not possible, but the blade is unusual for British representatives of *Cavusgnathus* in that the denticles decrease in height posteriorly. Species reported from Britain show an increase in denticle height posteriorly, the blade terminating in a prominent cusp, as, for example, in *C. regularis* Youngquist and Miller and *C. naviculus* (Hinde) (see Higgins 1975, pl. 8, figs. 1-5, 12, 13). Other specimens (Pl. 91, figs. 3, 4, 6-8) are too broken for specific determination, but all have their morphological counterparts in Carboniferous faunas. An exception is an ozarkodinan element (Pl. 91, fig. 9), which does not compare in detail with any described Carboniferous or Permian form.

It is evident that these collections represent conodonts derived from Carboniferous strata exposed at the time of the late Permian marine transgression. The source appears to have been of Viséan or Namurian age as conodonts recovered from local Westphalian marine bands show little similarity to our remanie material.

Nottinghamshire locality 282

Conodonts from the Brough borehole are broken and abraded, some being sub-rounded. Only a few are identifiable and those showing the best preservation are illustrated (Pl. 91, figs. 11-19). Several are fragments of platform elements, which are unlike those of Permian genera and indicate a Devonian source.

The most significant components of the collection are platform elements of *Polygnathus* and *Icriodus*. *Polygnathus* occurs in Devonian and Carboniferous faunas, but *Icriodus* is restricted to the Devonian. Our specimens of *Icriodus* clearly exhibit three rows of nodes on the platform and a large basal cavity occupying the entire lower surface. A coniform element from the same sample (Pl. 91, fig. 11) may also belong to *Icriodus*. Other ramiform specimens (Pl. 91, figs. 14, 15) are not diagnostic of a Devonian age, but elements of comparable morphology are common in Devonian faunas.

Strata of Carboniferous age occur widely in the area around Nottinghamshire, and provide ready sources for the derived Carboniferous specimens found in north-west Nottinghamshire. The origin of these Devonian conodonts is more problematical. There is at present no outcrop of

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EXPLANATION OF PLATE 90

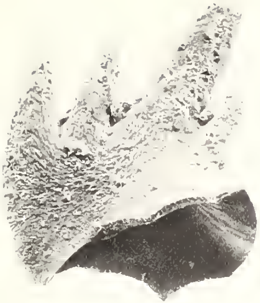
Figs. 1, 2. *Merrillina divergens* (Bender and Stoppel). 1, lateral view of MPK 3123, × 100. 2, lateral view of MPK 3124, × 100. Both specimens from 283/4.

Figs. 3, 5-15. *Ellisonia* spp. 3, inner lateral view of Pb? element MPK 3125, × 100, 283/1. 5-7, inner lateral views of Sc elements MPK 3127, MPK 3128, MPK 3129; all specimens × 60, 283/4. 8, lateral view of Sa element MPK 3130, × 100, 283/1. 9, 10, 14, inner lateral views of M elements MPK 3131, × 150; MPK 3132, × 150; MPK 3136, × 100. All specimens from 283/4. 11, inner lateral view of Sa/Sb element MPK 3133, × 100, 283/1. 12, 13, inner lateral views of Sc elements MPK 3134, × 100, 283/1; MPK 3135, × 150, 283/3. 15, inner lateral view of Sb element MPK 3137, × 150, 283/1.

Fig. 4. *Ellisonia* cf. *E. triassica* Müller, Prioniodinan element. Inner lateral view of MPK 3126, × 60, 283/3.

Fig. 16. Indeterminate P element. Upper view of MPK 3138, × 150, 283/5.

Repository of specimens on this plate: Institute of Geological Sciences, Ring Road, Halton, Leeds.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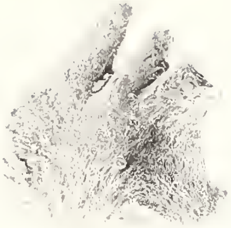
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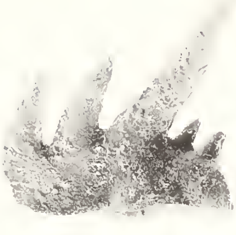
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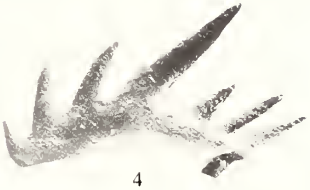
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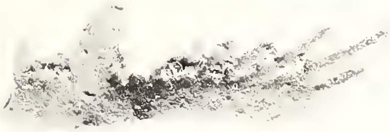
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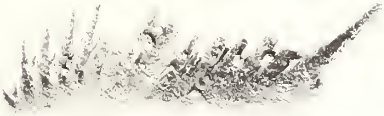
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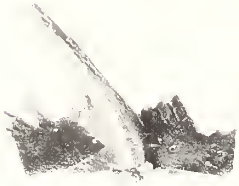
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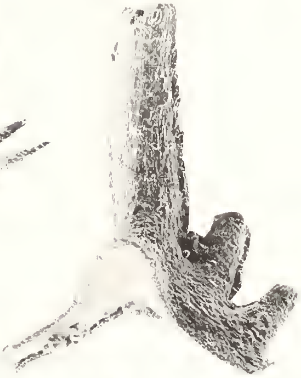
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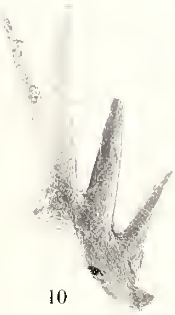
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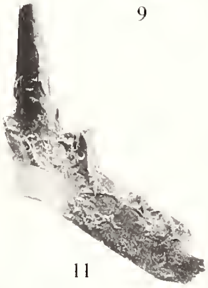
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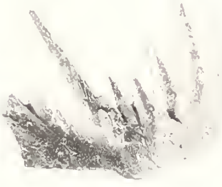
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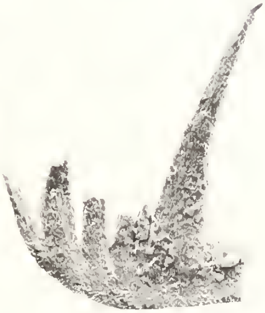
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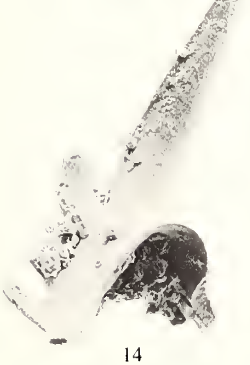
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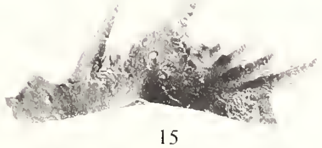
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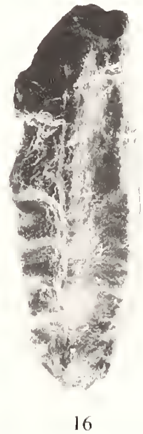
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SWIFT and ALDRIDGE, Upper Permian conodonts marine Devonian rocks nearer than North Devon, but borehole evidence has demonstrated sub-surface marine Devonian strata beneath areas of south-east and south central England. Wills (1973) cited sub-surface occurrences of probable marine Devonian as far north as Gayton, Wyboston, Cambridge, Soham, and Attleborough (text-fig. 1). More recently, possible marginal marine Devonian sediments have been recovered from a borehole near Hemington, 40 km north-west of Cambridge (Allsop and Jones 1981). Possible marine Devonian strata have also been encountered at depth in the Whittington Heath (Mitchell 1954) and Merevale boreholes. Nearer our Brough locality, the Dukes Wood No. 146 borehole at Eakring (Lees and Taitt 1946) passed through conglomerates and sandstones of Old Red Sandstone facies and possible Devonian age (text-fig. 2A).

In many of the borehole sequences the Devonian deposits are succeeded by Carboniferous rocks, showing that they would not have been exposed during the Permian. Only at Wyboston, Hemington, Soham, and Attleborough does the Devonian directly underlie Mesozoic formations. Nowhere in this northern extension of the Devonian sea is there evidence of open marine faunas, whose nearest proven occurrence is in the Steeple Aston borehole of Oxfordshire (text-fig. 1), drilled by the Institute of Geological Sciences (Poole 1977). Macrofossils and microfossils there indicated a late Devonian age, and three samples of sandy limestone yielded on digestion conodont faunas characterized by *Polygnathus* and *Icriodus* (Reynolds, *in* Poole 1977), an association broadly similar to that present at Brough. Although the Devonian sequence in the Steeple Aston borehole is overlain by nearly 550 m of Upper Coal Measures and igneous intrusives, it does demonstrate that open marine conditions prevailed in this region in the late Devonian.

There is thus no evidence for a local source of our derived Devonian conodonts. It seems probable that they were carried into the Zechstein sea by fluviatile transport from Devonian outcrops at least some tens of kilometres to the south. The lack of any admixture of Carboniferous forms suggests that the transporting river did not cut any major Carboniferous outcrops, but presumably flowed over the Lower Palaeozoic and Precambrian basement that underlies much of the east Midlands (Wills 1973).

EXPLANATION OF PLATE 91

Fig. 1. *Metalonchodina* cf. *bidentata* (Gunnell). Inner lateral view of 3664/13, × 150, 277/5.

Fig. 2. *Spathognathodus*? cf. *S. campbelli* Rexroad. Lateral view of 3220/18, × 150, 277/1.

Figs. 3, 4. *Ozarkodina* sp. A. 3, lateral view of 3662/3, × 150, 277/2. 4, lateral view of 3661/0, × 150, 278/5.

Fig. 5. *Neoprioniodus* cf. *singularis* (Hass). Inner lateral view of 3662/2, × 150, 278/5.

Fig. 6. *Hindeodella* sp. Lateral view of 3665/15, × 100, 277/1.

Fig. 7. *Spathognathodus*? sp. Lateral view of 3664/12, × 150, 277/4.

Fig. 8. *Synprioniodina*? sp. Inner lateral view of 3661/1, × 150, 278/5.

Fig. 9. *Ozarkodina* sp. B. Lateral view of 3221/15, × 150, 278/5.

Fig. 10. *Cavusgnathus* sp. Inner lateral view of 3663/6, × 150, 277/2.

Fig. 11. Coniform element. Inner lateral view of 3985/9, × 150, 282/1.

Figs. 12, 13, 16. *Polygnathus* spp. 12, upper view of 3672/9, × 100. 13, upper view of 3669/41, × 150. 16, upper view of 3671/4, × 150. All specimens from 282/1.

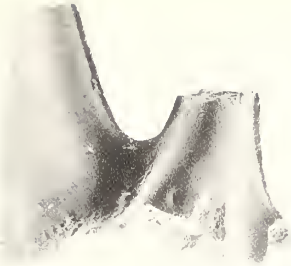
Fig. 14. Ramiform element A. Inner lateral view of 3671/6, × 100, 282/1.

Fig. 15. Ramiform element B. Inner lateral view of 3670/1, × 150, 282/1.

Figs. 17–19. *Icriodus* spp. 17, upper view of 3671/7, × 100. 18, upper view of 3672/8, × 150. 19, upper view of 3670/3, × 150. All specimens from 282/1.

Repository of specimens on this plate: Conodont Reference Collection, Department of Geology, University of Nottingham.

PLATE 91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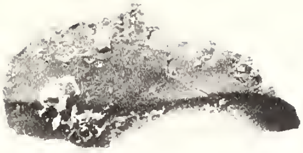
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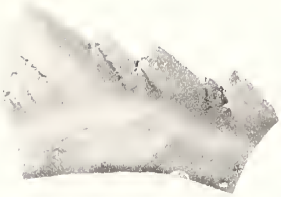
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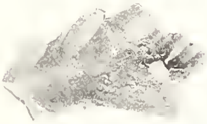
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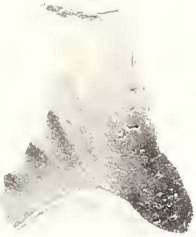
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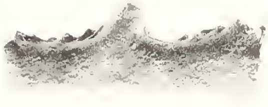
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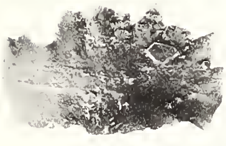
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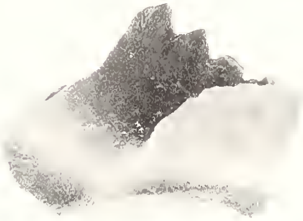
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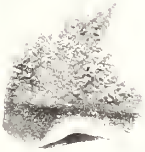
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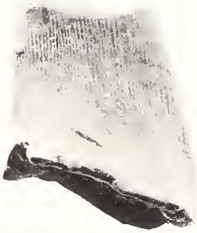
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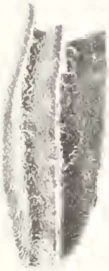
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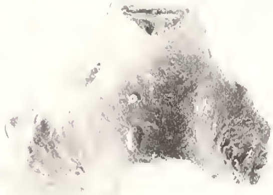
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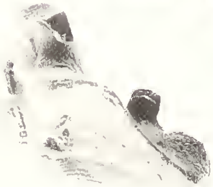
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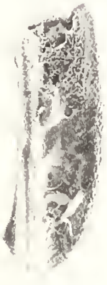
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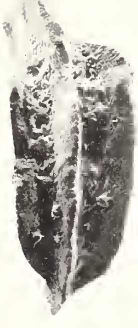
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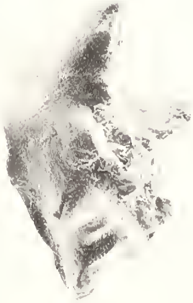
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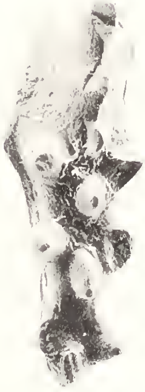
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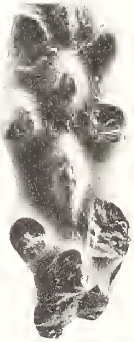
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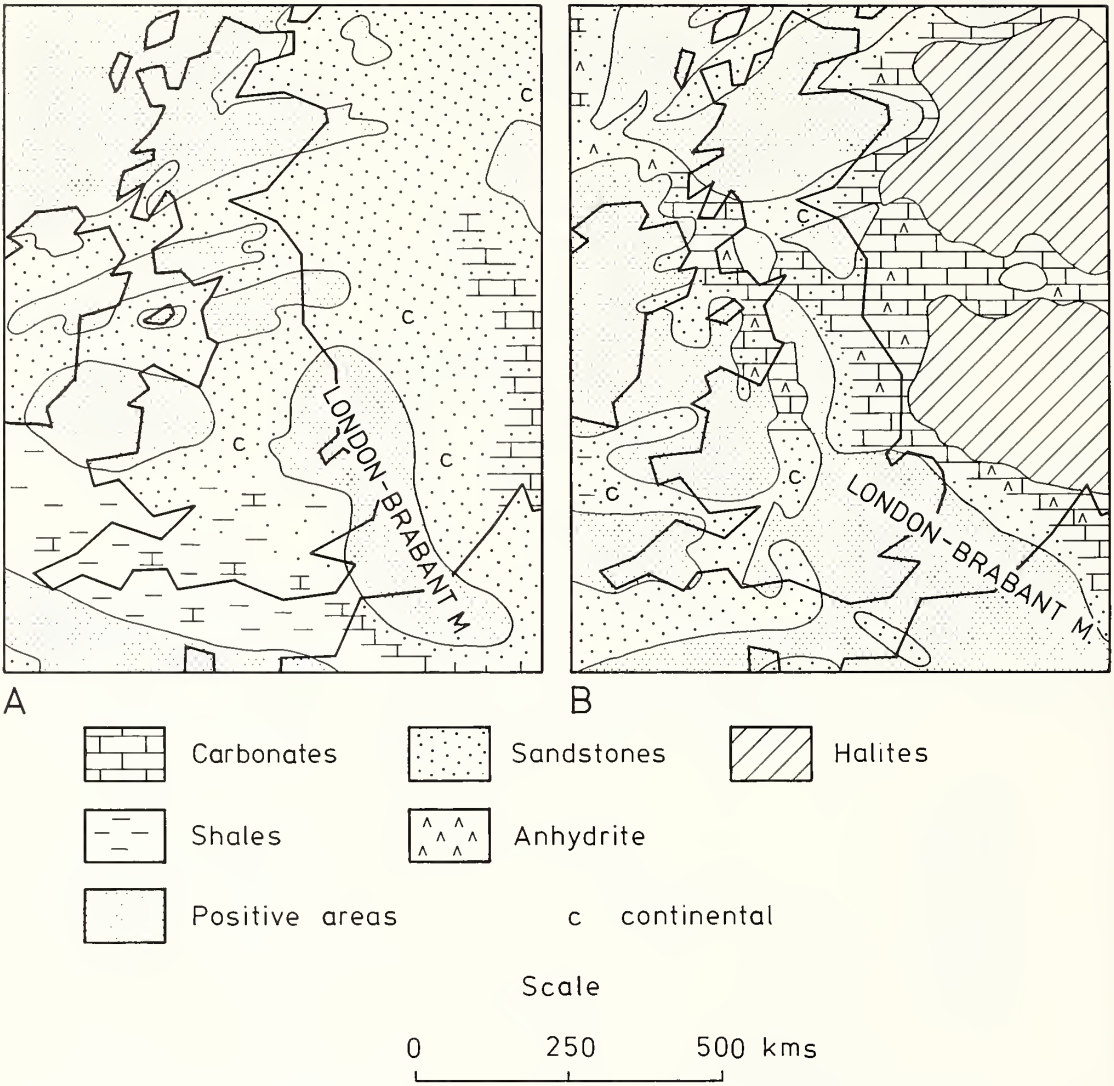
SWIFT and ALDRIDGE, Upper Permian conodonts



TEXT-FIG. 2. Palaeogeographical maps of Britain during the late Devonian (A) and late Permian (B); after Ziegler (1981), with modifications.

CONCLUSIONS

Identifiable conodonts are shown for the first time to occur in the Upper Permian of Britain, although all the collections recovered are low in both numbers and diversity. Marginal deposits of the Zechstein basin (text-fig. 2B), such as those of Nottinghamshire, are more likely to contain conodonts redeposited from older strata than indigenous faunas. Our recovery of indigenous specimens from Zechstein 1 strata of North Yorkshire indicates that further investigations in the Yorkshire and Durham areas offer the best prospects of producing additional Permian faunas from Britain.

Acknowledgements. Financial assistance towards collecting and processing samples from Nottinghamshire was provided as a research grant by the Nottinghamshire County Council. We are grateful to the Institute of Geological Sciences, particularly Mr. J. Pattison and Dr. D. W. Holliday, for providing material and stratigraphic information. The following sections of the National Coal Board are thanked for providing access to borehole cores: the East Midlands Geological Service, the National Exploration Unit, and the North-East Area Office; Mr. M. Nutting of the N.C.B. also provided field guidance and stratigraphic information. Dr. A. C. Higgins and Dr. M. J. Orchard commented valuably on the conodonts; Dr. D. B. Smith and Professor W. C. Sweet read the manuscript and suggested several improvements. Scanning electron micrographs were taken at the Wolfson Institute for Interfacial Technology with the assistance of Mr. L. Green. We also thank Mrs. J. Wilkinson and Mr. D. Jones for cartographic and photographic assistance respectively, and Mrs. J. Angell for typing.

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SHELL STRUCTURE OF THE DEVONIAN RETZIID BRACHIOPOD *PLECTOSPIRA FERITA*

by GERTRUDA BIERNAT *and* ANDRZEJ BALIŃSKI

ABSTRACT. Electron microscope studies of *Plectospira ferita* (von Buch) show the presence of two inorganic layers, primary and secondary, as well as a third, outermost one interpreted here as a periostracum. This is the first time a periostracum has been recognized in the fossil state. The structure of the periostracum of *P. ferita* is described and a comparison is made with periostraca of living brachiopods. The micro-ornamentation of the shell of *P. ferita* is described; pits and tubercles occurring on the surface of the primary layer are considered in detail.

THE minute Middle Devonian retziid brachiopod *Plectospira ferita* is a remarkable, but poorly known, species originally described by von Buch (1834). One of its characteristics is a differentiated surface ornamentation. The shell is folded with a zig-zag anterior commisure and bears distinct and numerous trunk-like surface tubercles. The most interesting are very fine, densely spaced pits looking like puncta (text-fig. 1).

No detailed observations were made during study of the Middle Devonian brachiopods from the Holy Cross Mountains (Biernat 1966) because this species is very rare in the Devonian of Poland, being then known from only one specimen. Since 1966 only three additional shells have been found during field-work, one of them with an exceptionally well-preserved shell exterior. This shell, together with some others of the same species from West Germany, have allowed detailed electron microscopic studies.

Material

The collection studied includes specimens of *P. ferita* (v. Buch) from Poland and West Germany. The specimens from Poland come from brachiopod-bearing marly shales of the Skały Beds, Holy Cross Mountains (exposure 83), where they occur together with other rare brachiopods such as *Uncinulus primipilaris* (v. Buch), *Kayseria lens* (Phillips), *Undispirifer* sp., *Cyrtina intermedia* (Oehlert), *Squamulariina parva* (Gürich) (see Biernat 1966, text-figs. 1-3). One of the four Polish specimens of *P. ferita*, the best-preserved of those studied up to now, has been broken into small pieces and investigated with the SEM.

Nine out of forty-nine specimens from the Middle Devonian of Eifel, West Germany, have been studied with the SEM. They are not so well preserved, usually with an exfoliated primary shell layer. In some specimens the primary layer is preserved only in the form of small patches between the ribs in the anterior part of the shells. Complete shells as well as sections and fragments of shells have been studied. The specimens from West Germany are housed at the Palaeontological Museum of the Humboldt University in Berlin (cat. nos. MB. B 303-306). The specimens from the Holy Cross Mountains are housed at the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw (cat. no. ZPAL Bp VII).

SHELL STRUCTURE OF *PLECTOSPIRA FERITA*

Shell structure of *P. ferita* is easily comparable with that of other Spiriferida. What is more, exceptionally well preserved specimens of this species enable correlation of each shell layer with

[Palaeontology, Vol. 25, Part 4, 1982, pp. 857-867, pls. 92-95]

particular stages of exoskeletal secretion in the Recent brachiopods, including an initial stage of forming an outermost organic sheet.

The specimens under study reveal two inorganic layers, the primary and the secondary ones, the latter being endopunctate. A most exciting and interesting discovery is the recognition of the third, outermost layer, which probably corresponds with the outermost organic layer of the Recent brachiopods, i.e. the periostracum. It is preserved either as a very thin layer overlying the calcitic primary layer and/or as more or less circular isolated patches filling the cup-shaped pits on the primary layer (e.g. Pl. 92, figs. 2–5).

A preserved periostracum within the Palaeozoic brachiopods is a new record. There is no other evidence for such a layer, except for the moulds of protegular parts of periostracum on some inarticulate brachiopods (Biernat and Williams 1970; Poulsen 1971). However, one can suggest that the preservation of periostracum on fossil brachiopods is not so rare. The specimens of *P. ferita* from West Germany kindly loaned to us by the Palaeontological Museum of the Humboldt University in Berlin also possess similarly preserved periostracum.

The shell exterior is covered by tubercles—a characteristic shell ornamentation for *P. ferita*. Depending upon the state of preservation, the shell surface can be ornamented also by pits or patches of periostracum filling them (Pl. 92, figs. 2, 4; Pl. 95, fig. 1).

Primary layer. The outer surface of the primary layer is finely granular without evident traces of the radial lineation described in some Spiriferida (Mackinnon 1974, p. 193, pl. 1, figs. 1, 4; pl. 15, fig. 4). Such lineation only rarely occurs in *P. ferita* and may be partly due to some recrystallization and weathering (Pl. 92, fig. 1).

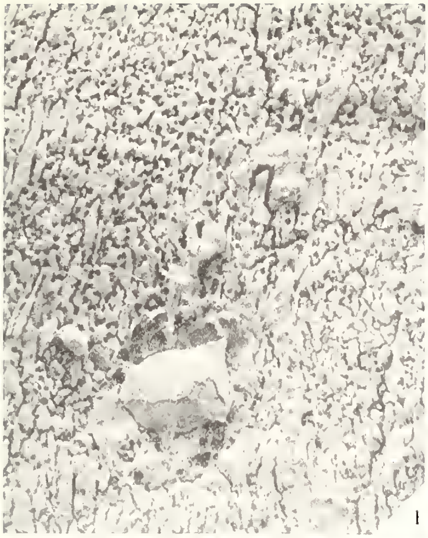
The thickness of the primary layer can vary from about 17 to 35 μm, without taking into account the pits and tubercles. It is composed of crystallites having their long axes more or less normal to the plane of junction between the primary and secondary layers (Pl. 93, fig. 1). Fine depositional banding with a periodicity of about 0·3 to 0·8 μm occurs sporadically. This banding may be explained by diurnal changes in the rates of deposition, as is the case in Recent, and some fossil articulate brachiopods (Williams 1968*a*; Mackinnon 1974).

Secondary layer. The structure of the secondary layer of *P. ferita* strongly resembles that of other spiriferides. This layer is made up of stacked fibres which measure up to 20 μm in width. Fibres may exhibit a fine banding with a periodicity of about 0·3 to 0·6 μm, which may be the daily amount of deposition. The inner surface of the secondary layer shows a standard secondary shell mosaic pattern. The secondary layer contains lenses of coarsely crystalline calcite which can pass peripherally into standard fibrous calcite (Pl. 92, fig. 6). The endopunctate condition greatly resembles that of other Retziidina and Recent Terebratulida. The puncta are widely spaced, very thin, and measure 3 to 8 μm in diameter (Pl. 93, fig. 2).

Periostracum. Well-preserved specimens show a third layer overlying the calcitic primary shell layer. The third layer is very thin, usually reaching a thickness of 1·5 to 2·0 μm (Pl. 93, fig. 1); exceptionally, it can be as thick as 6 μm.

EXPLANATION OF PLATE 92

Figs. 1–6. *Plectospira ferita* (von Buch). 1, view of the external surface of the primary layer showing traces of fine radial lineation (running from bottom to top). × 600. ZPAL Bp VV/663a. 2, view of slightly inclined external surface of primary layer showing patches of periostracum filling cup-shaped pits; an empty pit at top left corner. × 600. MB. B 303. 3–6, ZPAL Bp VII/663a: 3, view of fragmentarily preserved periostracum overlying the granular surface of the primary layer; lamellar structure well seen at the right of micrograph. × 1000. 4, view of the external surface of shell showing patches of petriostracum and two tubercles. × 100. 5, view of the external surface of shell showing the formation of patches of periostracum. × 300. 6, section through a tubercle showing the primary (top) and secondary layers; the latter with a lens of coarsely crystalline calcite (bottom of micrograph). × 300.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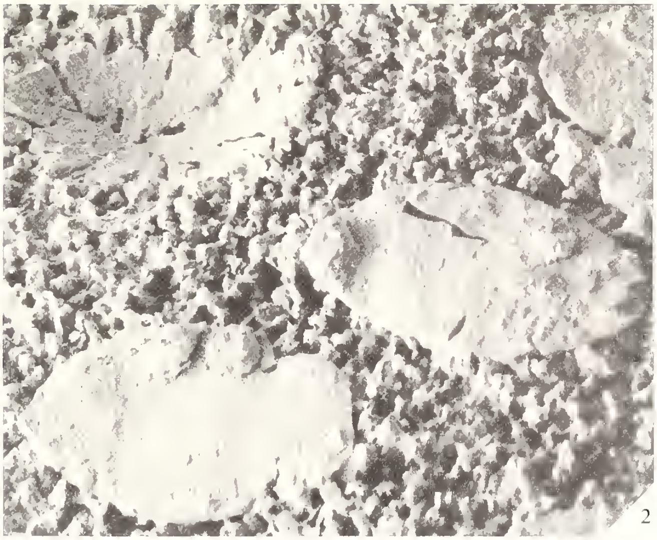
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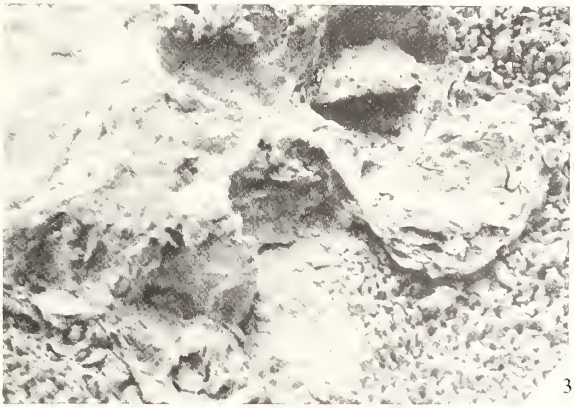
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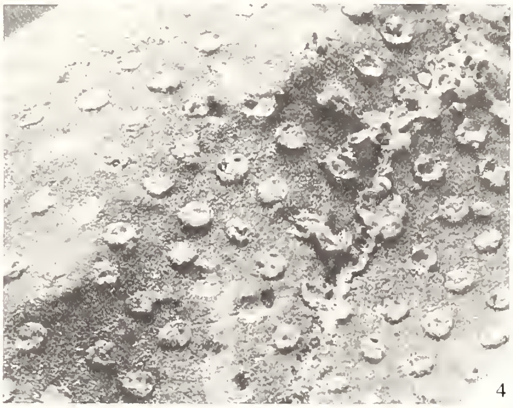
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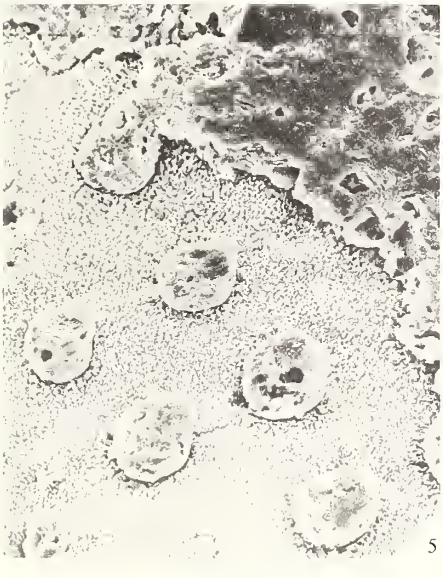
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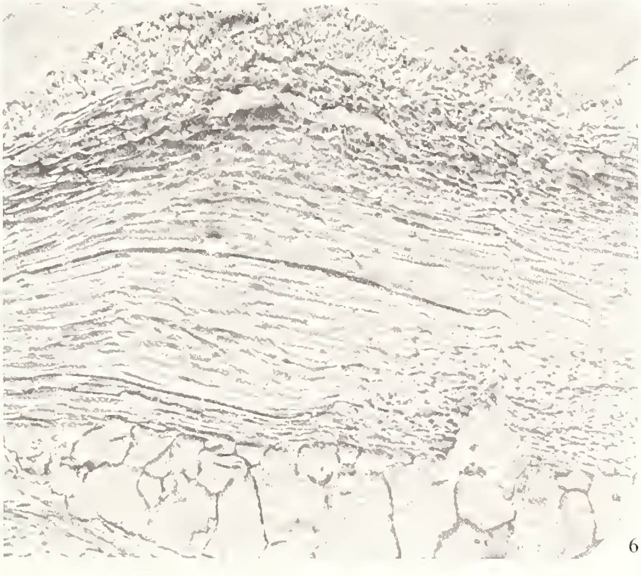
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In the specimens of *P. ferita* from West Germany, the primary structure of the outermost thin layer is obliterated (Pl. 92, fig. 2). More details on the structure of this layer can be seen on the well-preserved specimen from the Holy Cross Mountains. Here the outermost layer shows a distinct lamellar structure (Pl. 92, fig. 3; Pl. 94, fig. 2). The lamellae are about 0·1 to 0·2 μm thick. There are also sporadic, fine vesicles approximately 1 μm in diameter.

A somewhat different structure is to be found in characteristic hemispherical or somewhat lens-like thickenings of the outermost layer, which fill in the pits on the primary layer. Alongside thin lamellae there are numerous vesicles. They show wide variation in size, but extremely large vesicles, up to 20 μm or more in diameter, are typical (Pl. 92, figs. 3, 5–6; Pl. 94, fig. 6). The base of the hemispherical thickenings is formed by a somewhat thicker lamella, which pads the smooth surface of the pit bottom on the primary layer (Pl. 93, fig. 4; Pl. 94, fig. 1). This smooth surface of the pits (Pl. 94, fig. 3) suggests that the inner padding lamella was strongly cemented to the pit bottom, unlike the rest of the junction surface of the outermost and primary layers. This may explain, at least in part, the formation as a result of weathering of characteristic patches of the outermost layer on the surface of the primary one (Pl. 92, figs. 4–5).

Origin of the outermost layer

On the basis of the morphology described above it seems most likely that the third, outermost layer corresponds to the periostracum. The thickness of periostracum in Recent brachiopods rarely exceeds a micron, but in *Macandrewia* it can attain more than 8 μm (Williams and Mackay 1978, 1979). The thickness of periostracum of *P. ferita*, although undoubtedly much reduced during fossilization, could fall within these limits.

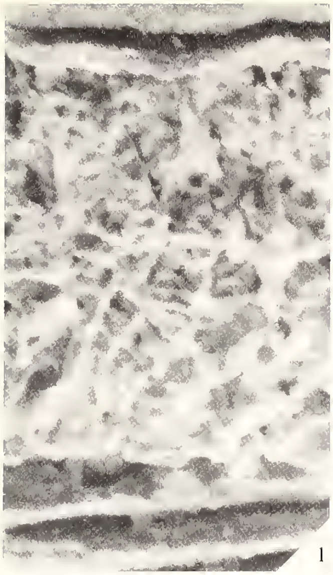
The recognized structural elements of this layer—such as lamellae and vesicles—can be compared with analogous structures of the known periostraca of Recent brachiopods.

One of the essential arguments convincing us that the layer in question can be interpreted as a periostracum is its place in the exoskeletal secretory regime of *P. ferita*. As has been shown by studies on the ultrastructure of the calcareous shell of living and fossil articulate brachiopods, that part of the secretory regime has been remarkably stable throughout the known history of this group of brachiopods (Williams 1968*a*, *b*; Mackinnon 1974). Moreover, secretion of an outermost organic sheet must always have been an integral phase of the entire secretory regime (Williams 1968*b*, p. 1). From this point of view, the outermost thin layer covering the primary shell layer of *P. ferita* can correspond only with the outermost organic sheets of other brachiopods.

As far as we know, a preserved periostracum has never been observed in fossil brachiopods. The periostracum mentioned by Ivanova (1971, pp. 14–15) for a number of fossil brachiopods in fact corresponds to the calcitic primary layer. Jope (1965, 1969), on the other hand, recognized proteinaceous fragments from decalcified fossils of inarticulate and articulate brachiopods. There have also been reports of organic matrices in other fossil invertebrates, for example, ammonoids and pelecypods, some of them remarkably well preserved (e.g. Grégoire and Voss-Foucart 1970; Grégoire and Teichert 1965; Grégoire 1966; Erben, Flajs and Siehl 1969; Mutvei 1969; Pugaczewska 1976).

EXPLANATION OF PLATE 93

Figs. 1–7, *Plectospira ferita* (von Buch). 1, section through the secondary (bottom) and primary layers and a thin periostracum (top). × 2000. ZPAL Bp VII/663a. 2, section through the primary (top) and secondary layers showing punctum. × 1000. MB. B 304. 3–7, ZPAL Bp VII/663a. 3, fracture through a patch of periostracum filling a pit on the primary layer. Secondary layer at the bottom half of micrograph. × 1000. 4, view of the abraded patch of periostracum showing well-developed inner sealing membrane. × 1000. 5, view of the slightly abraded patch of periostracum showing its lamellar-vesicular structure. × 1500. 6, general view of a patch of periostracum showing a few slightly damaged large vesicles. × 1000. 7, more detailed view of the vesicle-bounding membrane. × 10K.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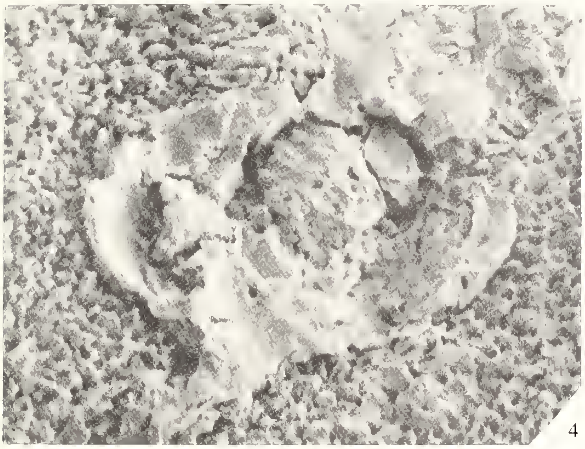
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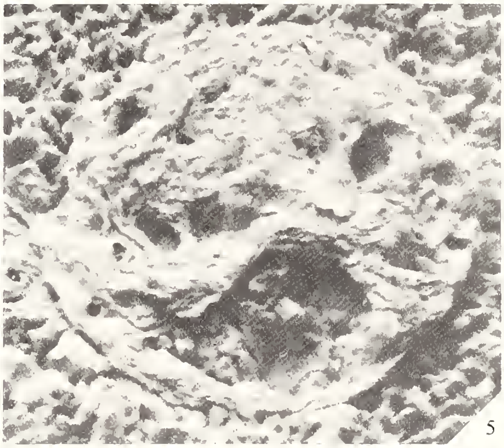
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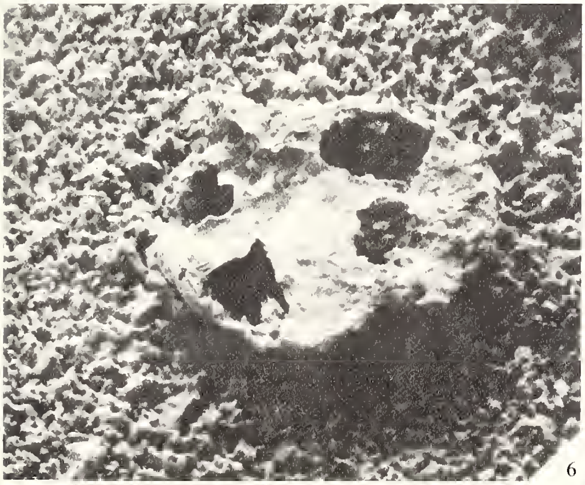
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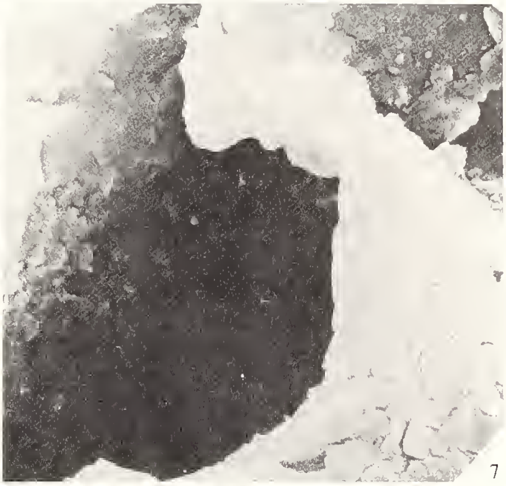
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This allows the supposition that the preservation of periostracum in fossil brachiopods is also to be anticipated if the right preservation is available. More attention must be paid in future to the shell surface when studying existing fossil collections. The periostracum may be preserved as its original material, with some diagenesis; it may also have undergone pseudomorphosis or impregnation, still preserving some of its original structure. This latter case may be exemplified by *P. ferita*.

Discussion

The present studies on periostracum of *P. ferita*, although fragmentary, throw some light on the degree of differentiation of the organic exoskeleton within the brachiopods. The lamellar structure recognized in the periostracum investigated may, to some extent, reflect its original structure. Particular lamellae may correspond to some of the periostracal elements of living brachiopods, such as the outer and inner bounding membranes (or basal membrane), the fibrillar mat, as well as the protein labyrinth changed due to compaction and the vacuoles bounded by triple-layered membranes (Williams and Mackay 1978, 1979).

Small vesicles in the periostracum of *P. ferita* correspond presumably to the mucin inclusions and vacuoles (Williams 1968*b*). But hemispherical periostracal thickenings densely and regularly distributed have not, so far, equivalents within the known periostraca of Recent brachiopods. The presence of such structural elements is suggestive of further possibilities both in specialization and secretory differentiation of the mantle edge cells. As the best-preserved fragments of the shell from Poland show, these thickenings appear to be made up, in their greater part, of vesicular tissue (Pl. 93, figs. 5–7; Pl. 94, fig. 6), underlain by a thickened inner sealing membrane (Pl. 93, fig. 4; Pl. 94, fig. 1). Among living articulates a vesicular periostracum is the more prevalent condition (Williams 1968*c*, p. 274; 1968*b*, p. 8; Biernat and Williams 1970, p. 502). However, the vacuoles of the periostracum within living brachiopods may approach about 3 μm in diameter, in contrast to *P. ferita*, where they may be more than 20 μm. If these vesicles really correspond to the original structure of the periostracum, they may be treated as a secretory result of a few, or perhaps of many cells. By comparison with the vacuoles in Recent forms, these vesicles must have contained the discarded cell constituents, and in all probability were bounded by triple-layered membranes.

ORNAMENTAL FEATURES OF THE MINERAL SHELL SURFACE

Pits

Pits, which are moulds of hemispherical thickenings of periostracum on the surface of the primary layer (Pl. 93, fig. 2), constitute one of the most characteristic elements of micro-ornamentation of the mineral shell surface (Pl. 95, fig. 1). Their distinctness and appearance depend very much upon the state of preservation of periostracum. The most common is the case when the shell is devoid of periostracum and the pitted surface of the primary layer is then well seen. Pits, densely spaced over the whole shell surface, are arranged in regular oblique rows (Pl. 95, fig. 1). Their regular concavity shows only little variation in outline from rounded to longitudinally elliptical, ranging from 45 to

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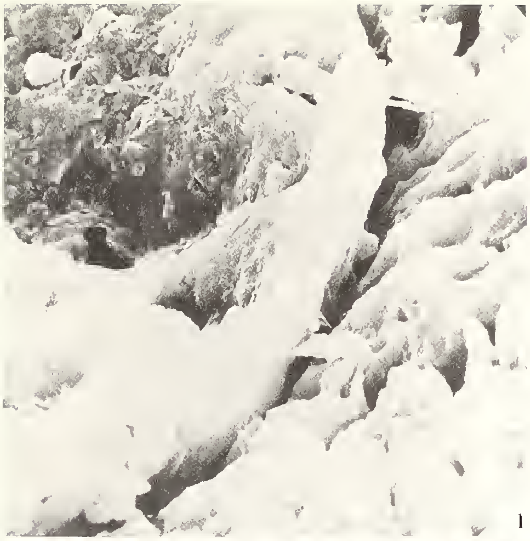
EXPLANATION OF PLATE 94

Figs. 1–7, *Plectospira ferita* (von Buch). 1, detailed view of edge of a patch of periostracum showing the inner sealing membrane. × 3600. ZPAL Bp VII/663a. 2, detailed view of a fragment of periostracum showing its lamellar structure. × 10K. Same specimen as fig. 1. 3, view of a pit on surface of the primary layer with well-preserved smooth pit bottom. × 600. MB. B 303. 4-7, ZPAL Bp VII/663a. 4, view of a pit with somewhat weathered bottom showing a characteristic rosette-like pattern of crystalline arrangement. × 1000. 5, section through a pit showing arrangement of crystallites of the primary layer (top). Secondary layer at bottom half of micrograph. × 1000. 6, view of a patch of periostracum showing its vesicular-lamellar structure. × 1500. 7, external view of the primary (top) and secondary layers; a part of the pit is seen in the centre; notice the lack of connection between the pit and endopunctation. × 1000.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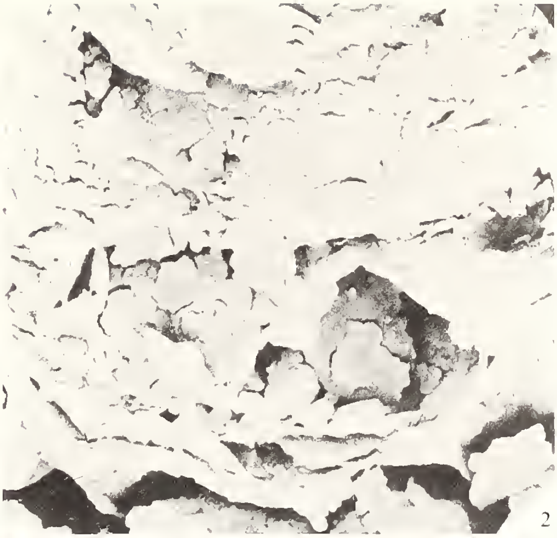
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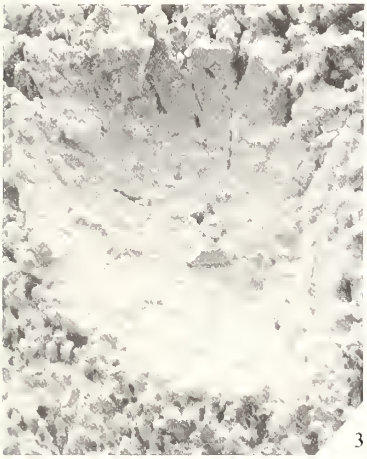
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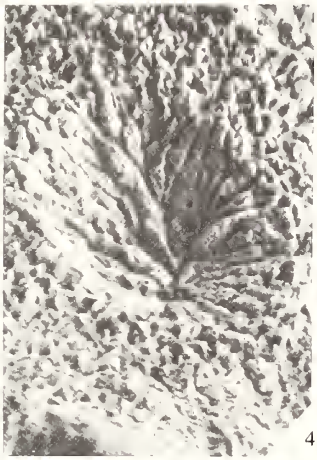
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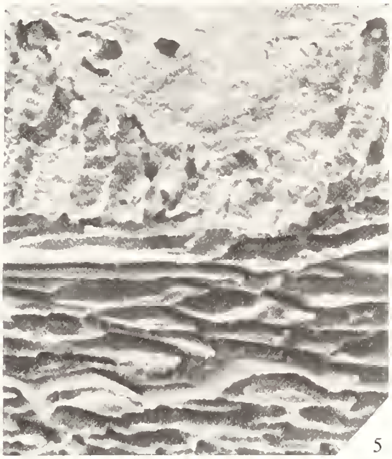
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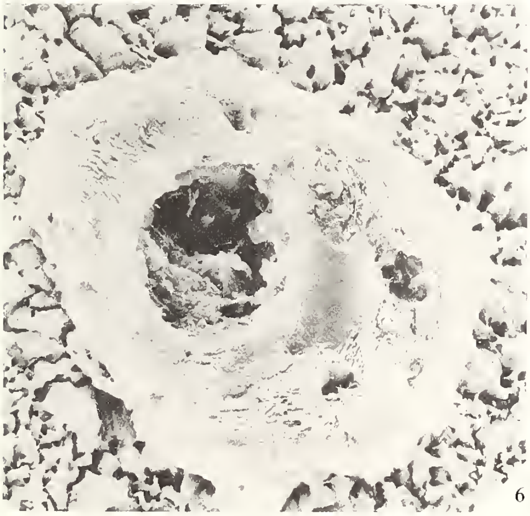
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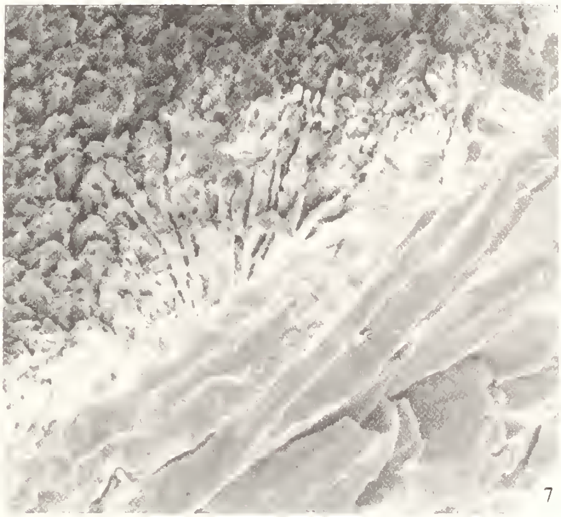
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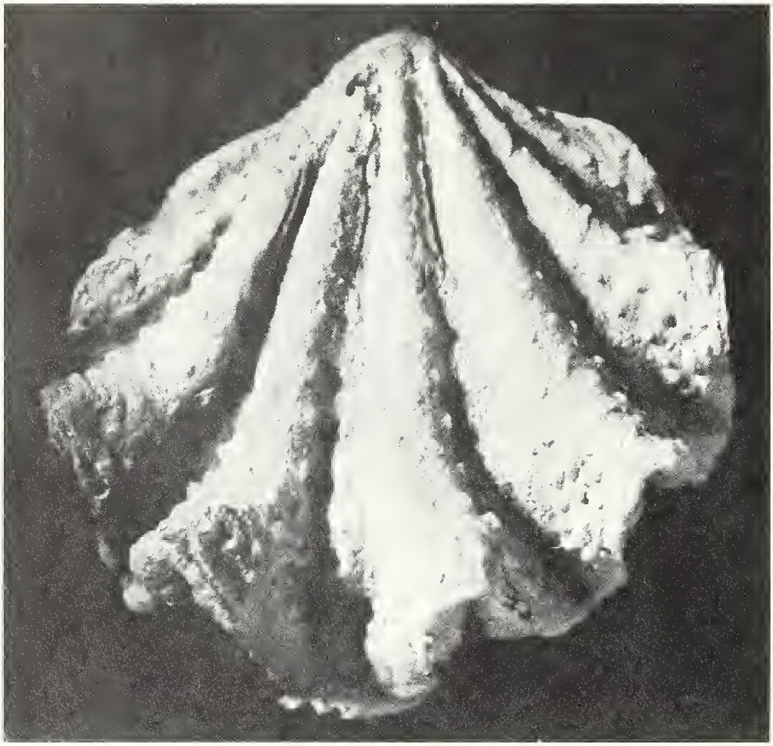
75 μm in diameter and from 12 to 17 μm in depth. The bottom of the pit, if well preserved, can be smooth (Pl. 94, fig. 3), but if somewhat weathered it shows a rosette-like pattern (Pl. 94, fig. 4) because of a specific arrangement of crystallites of the primary layer (Pl. 94, fig. 5).

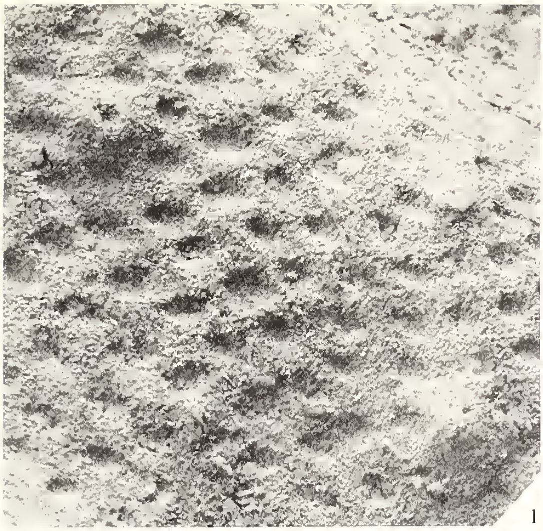
In many cases, however, the pattern of the shell surface is peculiar. There occur small patches of periostracum, similar to the pits in their arrangement and outline (Pl. 94, fig. 4). These patches are remnants of the periostracum that fills in the pits. Such a preservation is due to gradual weathering as well as to the disintegration of periostracum (Pl. 92, fig. 5). There are also a few places where the shell surface is smooth, being covered by periostracum which screens the presence of pits. It is worth adding that no connection between the pits and endopunctation has been recorded (Pl. 94, fig. 7).



TEXT-FIG. 1. Ventral view of a shell of *Plectospira ferita* (von Buch) showing its ornamentation. × 15. ZPAL Bp VII/663b.

EXPLANATION OF PLATE 95

Figs. 1–6. *Plectospira ferita* (von Buch). 1, view of the pitted surface of the primary layer and two tubercles. × 100. MB. B 306. 2, detailed view of a domed tubercle with an apical orifice. × 300. Same specimen as fig. 1. 3, detailed view of a trunk-like tubercle with a rosette-like pattern of arrangement of crystallites in its apical part. × 300. ZPAL Bp VII/663a. 4, view of a damaged tubercle with internal cavity. × 600. MB. B 306. 5, section through a tubercle showing the secondary shell layer penetrated by granular calcite, which is a continuation of the primary layer. × 300. MB. B 304. 6, section through a tubercle showing the succession of the primary and secondary layers. An orifice is seen in the apical part of the tubercle. × 300. Same specimen as fig. 5.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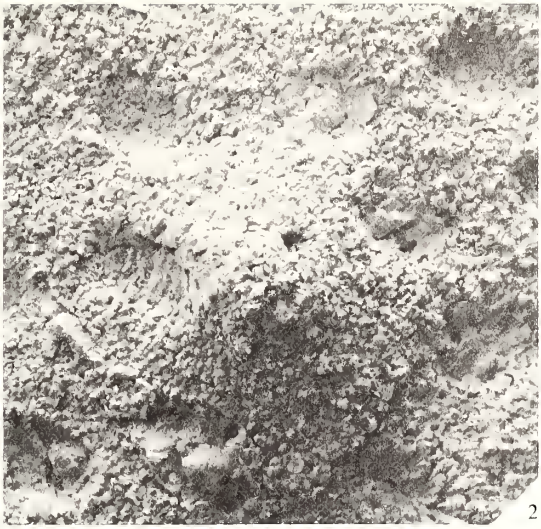
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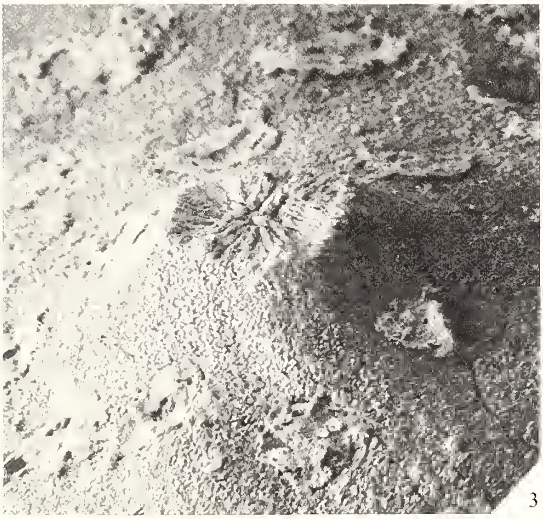
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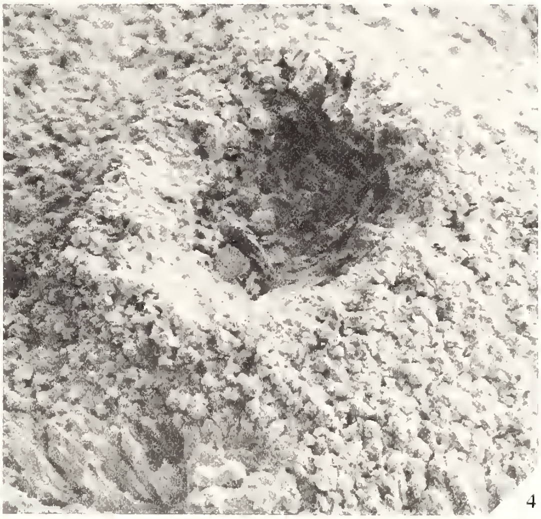
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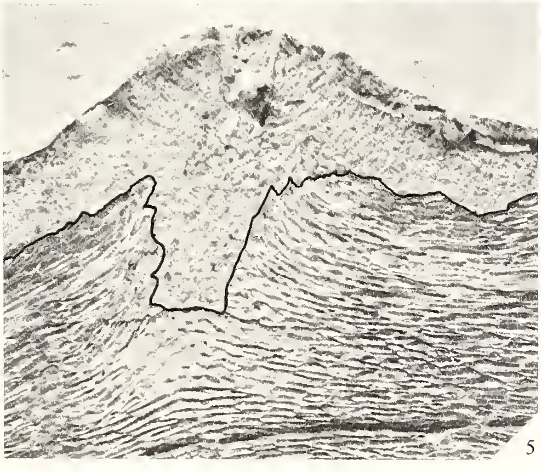
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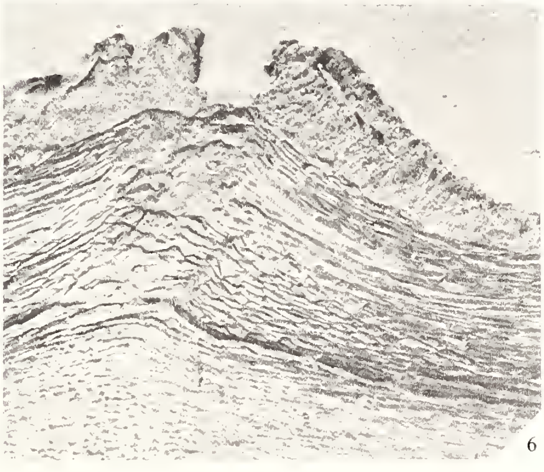
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Tubercles

These ornamental elements are developed as small trunk-like-to-domed outgrowths, on the average 200 μm in diameter and up to about 125 μm in height, arranged in a somewhat quincuncial pattern. They occur over the whole shell surface but are more densely spaced on the anterior half of adult shells (text-fig. 1). These outgrowths are made up of the primary layer with the secondary one protruding outwardly (Pl. 92, fig. 6; Pl. 95, figs. 5–6). Several types of structure are recognized, two being most common: *a*, tubercles of a slightly domed appearance with a small round orifice in the apical part (Pl. 95, figs. 2, 6); *b*, tubercles of trunk-like form possessing a wide funnel-like apical concavity; the bottom of this concavity displays a rosette-like pattern because of a radial arrangement of crystallites of the primary layer (Pl. 95, fig. 3).

The function of the tubercles still remains unclear. No doubt these elements are associated with highly specialized groups of cells of the outer epithelium of the mantle. These cells presumably acted as, for example, sensory organs, analogous to the sensory spines of some brachiopods. Considering the tubercles from that point of view, one may assume that they correspond to strongly reduced and shortened spines.

The tubercles may have an internal cavity (Pl. 95, fig. 4). In some of them the internal cavity is quite large and often filled in with granular calcite, which is a distinct continuation of the primary shell layer. This calcite may penetrate the secondary shell layer to a depth of about 100 μm (Pl. 95, fig. 5). No communication of the tubercles proper with the interior of adult shell has been indicated.

The differences observed in the structure of the tubercles may result, to some extent, from the unequal lengths of the period of their functioning during the growth of the animal. Probably the shortest was the functioning of those tubercles which show a radial arrangement of crystallites in their apical part (Pl. 95, fig. 3). Their activity must have terminated before the secretion of the fibres of the secondary layer began. The longest appears to be the functioning of the tubercles with a deep funnel-like canal filled in with the granular calcite and a protruding secondary layer (Pl. 95, fig. 5). In this case the cells of the mantle had to be retracted from the central canal of the tubercle merely within the time of the secondary-layer secretion. Outwardly deflected fibres of the secondary layer around the canal indicate that the granular calcite has been secreted much later than the fibres of the secondary layer.

The structure of tubercles suggests that they were functional near the antero-lateral valve margins only. During the growth of the shell the contact between the tubercles and the shell interior became cut off. Thus, the older and non-functional tubercles were then replaced by new ones formed continually at valve edges.

CONCLUSIONS

From the structure of the shell of *P. ferita*, we suggest the following:

1. The mineral punctate shell of *P. ferita* consisted of primary and secondary layers.
2. The outermost, thin layer recognized on the best-preserved specimens, and overlying the primary layer, is considered here as a periostracum. It is the first discovery of a preserved periostracum on fossil brachiopods.
3. The fossil periostracum of *P. ferita* consists mainly of lamellar and vesicular tissues.
4. Regular and densely distributed hemispherical thickenings of periostracum in *P. ferita* have no equivalents among known Recent brachiopod periostraca. This indicates further possibilities of structural differentiation and specialization of the cells of brachiopod mantle edges through their history.
5. The external surface of the primary layer is ornamented densely by pits which are the moulds of hemispherical thickenings of periostracum. The pits may be sometimes filled up with patches of disintegrated periostracum, resulting in a characteristic ornamentation of shell exterior.
6. The shell is covered by numerous tubercles which could have functioned as sensory organs.

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AFFINITY OF THE CAMBRIAN ALGA *TUBOMORPHOPHYTON* AND ITS SIGNIFICANCE FOR THE EPIPHYTACEAE

by ROBERT RIDING *and* LARISA VORONOVA

ABSTRACT. The problem of the true nature of the alga *Epiphyton* Bornemann and its allies centres upon the difficulty of recognizing features of affinity in these morphologically simple fossils. They have been compared with algae in a number of different groups, including, especially, florideophycidean rhodophytes. However, the general dimensions and shape of the Cambrian epiphytacean *Tubomorphophyton* Korde in specimens from Siberia suggest that it could be a bangialean rhodophyte, but details of its morphology and style of calcification are more consistent with its being a filamentous ensheathed cyanophyte. Its tubiform morphology is obscured in some specimens, probably due to the thickness of the calcified sheath material and to diagenetic alteration. This suggests that other epiphytaceans with apparently solid skeletons could be cyanophytes. Alternatively, the Epiphytaceae may be a heterogeneous group of algae superficially similar in gross morphology. These possibilities require reassessment of the nature and diversity of early Phanerozoic algal communities.

АННОТАЦИЯ. Проблема природы *Epiphyton* Bornemann и близких ему родов заключается в том, что в связи с простым морфологическим строением систематическая принадлежность их определяется с трудом. Размер и форма кембрийских *Tubomorphophyton* Korde в образцах из Сибири дают основание предполагать, что они могли быть филаментными (нитчатыми) цианофитами или эукариотными водорослями. Размер, морфология и кальцификация *Tubomorphophyton* дают возможность их относить к филаментным (нитчатым) цианофитам. Их трубчатая форма в некоторых образцах видна плохо скорее всего из-за толщины кальцифицированной оболочки, а это дает основание предполагать, что другие эпифитации, которые целиком состоят из микрозернистого карбоната, могли быть также скорее цианофитами, а не родофитами, как обычно считалось. Но эпифитации также могли быть гетерогенной группой водорослей, различных по своей природе, но сходной по макроморфологии. Каждая из этих возможностей требует переоценки природы и разнообразия водорослевых сообществ раннего фанерозоя.

THE Epiphytaceae Korde is one of the most distinctive and widespread algal groups appearing in the Lower Cambrian. These small but heavily calcified fossils, which characteristically form dendritic thalli a few millimetres in size, are prominent in shallow marine limestones of Cambrian age in Antarctica (Priestley and David 1910), Australia (Walter 1967), Europe (Bornemann 1886), North America (Ahr 1971; Handfield 1971), and the Soviet Union (Vologdin 1931, Korde 1955, 1959, 1961, 1973; Krasnopeeva 1955; Gudymovich 1967; Luchinina 1975; Reitlinger 1959; Voronova 1976; Drosdova 1980). They are commonly major rock-builders and alone, or in association with other algae and archaeocyathans, are important elements of Lower Cambrian bioherms. *Epiphyton* occurs in the Middle Cambrian of the Siberian Platform (Korde 1955, 1961) and the Middle Cambrian of the Altai-Sayan foldbelt (Stepanova 1974). It is common in the Middle Cambrian Cathedral Formation of British Columbia (McIlraeth 1977, p. 116) and is present in the Lower Ordovician of Kazakhastan (Voronova 1980). *Epiphyton*-like fossils, possibly *Angulocellularia* Vologdin (Riding and Voronova, *in press*), also occur in the Lower Ordovician *Calathium–Archaeoscyphia* bioherms of the south-western United States (Riding and Toomey 1972). *Epiphyton* reappears in Devonian stromatoporoid-dominated bioherms in several parts of the world (Chuvashov 1965; Antropov 1967; Wray 1977; Riding 1979*a*).

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Although Bornemann's (1886) original view that *Epiphyton* is probably an alga has not been seriously questioned, there has been no general agreement concerning the particular group to which it belongs. Bornemann (1886, pp. 16–17) thought it might be a chlorophyte but Pia (1927, p. 39) regarded it as a cyanophyte within the Porostromata; a view which Maslov (1956) endorsed, although with some uncertainty. Korde (1959) placed *Epiphyton* in yet another major algal group, the Rhodophyta, on the basis of her recognition of cellular microstructure and sporangia in specimens from the Cambrian of the south-eastern Siberian Platform. However, reservations have been expressed concerning the interpretation of these features (Maslov 1962; Voronova 1976; Wray 1977, pp. 41–42) and uncertainty remains concerning the affinity of *Epiphyton*. Apart from Korde, previous workers have not regarded specific features of *Epiphyton* and its allies as being distinctive of a particular group but have relied only on very general features in suggesting to which algal group they may belong. We propose here that one member of the Epiphytaceae, *Tubomorphophyton* Korde, has a distinctive morphology which is comparable with some bangialean rhodophytes, but which is more consistent with a cyanophyte affinity. If this tentative interpretation is extended to the Epiphytaceae as a whole, then it has a significant bearing upon our understanding of the early history of Palaeozoic algae because it suggests that a major group, often previously thought to be rhodophyte, is cyanophyte. If, on the other hand, *Tubomorphophyton* is regarded as distinct from *Epiphyton* and its relatives, then the implication will be that the Epiphytaceae is not a homogeneous group and that the diversity of Cambrian calcareous algae is greater than currently believed.

THE EPIPHYTACEAE

Epiphyton was originally described from the Cambrian of Sardinia by Bornemann (1886). Korde (1959) erected the family Epiphytaceae, comprising *Epiphyton* and *Chabakovia* Vologdin, and later (1961) established many new *Epiphyton* species. Subsequently, Korde (1973, p. 159) raised several of these to generic level and recognized the following ten constitutent genera within the Epiphytaceae: *Epiphyton* Bornemann, *Epiphytonoides* Korde, *Gordonophyton* Korde, *Kosvophyton* Korde, *Ludlovia* Korde, *Paraepiphyton* Wray, *Proninophyton* Korde, *Streptophyton* Korde, *Tharama* Wray, and *Tubomorphophyton* Korde.

Although the external bushy form of these fossils is distinctly plant-like, internal features of the calcareous skeleton which could be used to narrow the range of possible affinities are either lacking or equivocal. To most observers the skeleton appears to have a micritic ultrastructure without any features which might provide clues to its relationships, although Rozanov (1979, fig. 2, pp. 68–69) has noted the similarity between the micritic ultrastructures of *Epiphyton*, *Renalcis*, and archaeocyathans.

However, one member of the group, *Tubomorphophyton*, while retaining a micritic wall-structure, has a distinctly tubiform morphology. This is an important departure from the morphology to be expected if the Epiphytaceae as a whole had a skeletal structure similar to that of extant calcareous rhodophytes, in which the walls of individual cells are calcified and the organization is pseudoparenchymatous.

Both Luchinina (1975) and Wray (1977, p. 42) have recently considered that *Epiphyton* could be a cyanophyte. We enter the debate concerning its affinity to revive the older, more specific, opinion of Pia (1927) that allies of *Epiphyton* could belong to the Porostromata. This was foreshadowed by Gordon (1920, p. 684) when he described *E. fasciculatum* from the Antarctic as consisting of 'bifurcating tubules' and compared it with *Ortonella*. But, by basing our case on *Tubomorphophyton*, we believe it is stronger because, whereas most epiphytaceans are not clearly hollow, this genus has, as its name implies, a tubiform morphology comparable with that of filamentous cyanophytes, although it also resembles some rhodophytes. The problematic Reitlingerellidae (Loeblich and Tappan 1964, p. C787) is a group of tubiform calcareous microfossils but none of its members is comparable in form with *Tubomorphophyton*.

TUBOMORPHOPHYTON

All epiphytaceans show the dendritic form characteristic of the group, but their internal morphology ranges from rounded chambers and stacked discs to tubiform or apparently solid (Voronova 1976, fig. 21). To these features may be added the micromorphological details discerned by Korde (1959).

Tubomorphophyton is based on *E. botomense* Korde (1955) and the other members of the genus, *T. benignum*, *T. cristatum*, and *T. nubilum*, were also originally (Korde 1961) *Epiphyton* species prior to the erection of *Tubomorphophyton* (Korde 1973, p. 204). The feature which they share, and which distinguishes the genus, is the tubiform structure of the branches, although it should be noted here that the holotype of *T. benignum*, illustrated by Korde (1959, pl. 1, fig. 5) fails to show this character.

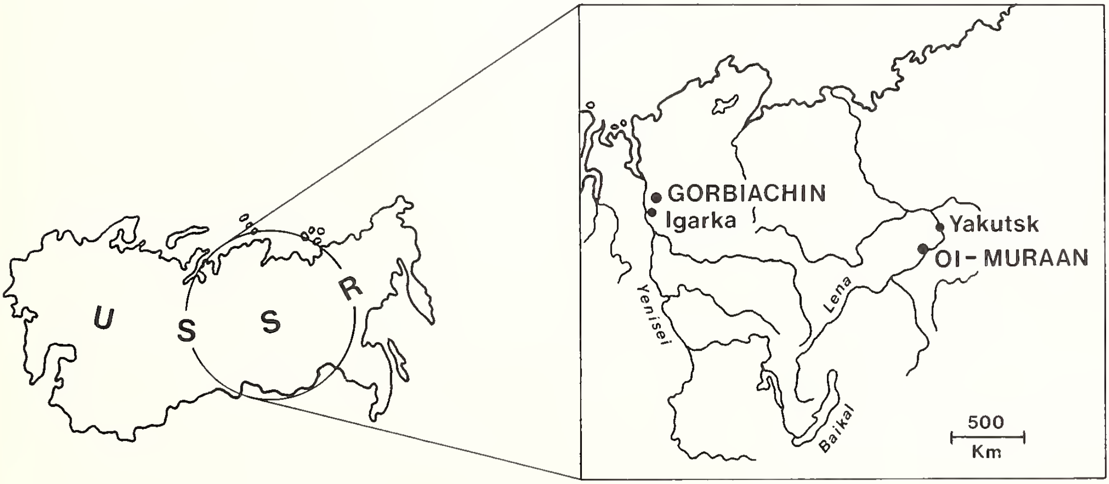
Tubomorphophyton has, so far, only been recorded from the Lower Cambrian of central and northern Asia. Korde (1973) describes it from the Lena River, Siberia, upstream from Yakutsk, and from the Kuznetskii Ala-Tau Mountains of the south-western Siberian Platform. The material described below is also from the Lena River and from a tributary of the Yenisei River further west.

Taxonomy

Korde (1961, 1973) has separated epiphytacean species on the basis of degree of branching, the angle and length of branches, the size of the thallus, and the diameter of filaments. In some cases the distinctions used are very fine and it can be difficult to satisfactorily follow the present taxonomy, a point which has been noted by Gudymovich (1967) and Luchinina (1975). The established species of *Tubomorphophyton* are so few in number (four) that they are easier to deal with: *benignum* and *cristatum* are relatively large forms and *cristatum* produces regular tufts branching at a low angle from the vertical; *botomense* has a slightly larger angle of branching; *nubilum* is a small form.

Material

The specimens described here are from the Lena and Gorbiachian Rivers of Siberia, USSR (text-fig. 1). They are of Lower Cambrian age, occurring in the Tommotian and Atdabanian Stages (text-fig. 2). The thin sections in which they occur are in the collections of the Palaeontological Institute (PIN) of the USSR Academy of Sciences, Moscow. Specimen B 927 (collection L. G. Voronova) is from the Gorbiachin River, a minor right-bank tributary of the Yenisei, and is of upper Tommotian age from the Krasny Porog Formation. Specimens B 70/25 and B 70/31 (collection L. G. Voronova) are from Oi-Muraan, a locality on the left bank of the Lena River, 3 km upstream from the village of Oi-Muraan (see Voronova 1976, p. 46 and fig. 23). This locality is between Zhurinsky Mys and Achchagy-Kyyry-Taas (see Cowie and Rozanov 1974, fig. 1). Specimen B 70/25 is of lower Atdabanian age from the Petrotsvet Formation. Specimen B 70/31 is also of Atdabanian age from the overlying Perekhod Formation.



TEXT-FIG. 1. Localities: Lena and Gorbiachin Rivers, Yakutia.

	TIME UNITS	LOCALITIES	
		Oi-Muraan	Gorbiachin
CAMBRIAN	Atdabanian	PEREKHOD ● B 70/31	KRASNY POROG ● B 927
		● B 70/25 PESTROTSVET	
	Tommotian		
PꞒ	Yudomian	YUDOMA	SUKHARIKHA

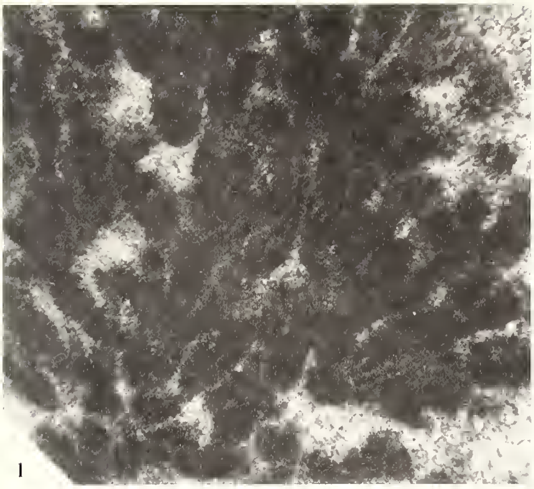
TEXT-FIG. 2. Stratigraphic position of the samples described here containing *Tubomorphophyton*. B 70/31 and B 70/25 both contain *T. botomense*. B 927 contains *T. benignum*. The Tommotian is currently regarded as the basal stage of the Cambrian, according to the preliminary recommendations of the International Working Group (Cowie 1978).

Morphology and dimensions

The specimens of *Tubomorphophyton* which we have examined are erect plants with short branches arising dichotomously and closely spaced to produce a dense tufted appearance (Pl. 96, fig. 1). There is no indication of a main axis. The filaments are of approximately constant diameter and are commonly seen to be hollow. The wall ranges in thickness from 3 to 34 μm, while the total tube diameter ranges from 23 to 91 μm. The tubular structure is seen most clearly in transverse sections (Pl. 96, fig. 2); in longitudinal sections the thickness of the wall, the thickness of the thin section, and the changing orientation of the skeleton combine to obscure the hollow interior, although this is nevertheless seen clearly in some specimens (Pl. 96, figs. 3, 4). In some cases the tube appears to close and reopen along the length of the filament, and branches with well-defined tubiform structure are juxtaposed against others which appear diffusely solid (Pl. 96, fig. 5). Our material contains both *T. botomense* (B 70/25 and B 70/31, Oi-Muraan) and *T. benignum* (B 927, Gorbiachin), the latter being distinctly larger. The fine structure of the skeleton appears to be featureless micrite (Plate 96, fig. 6). The tube interior is occupied by fine microsparite crystals.

EXPLANATION OF PLATE 96

Figs. 1–6. *Tubomorphophyton botomense* (Korde). 1, 3, 4, 6, sample PIN B 70/31, Perekhod Formation, Atdabanian; Oi-Muraan, Lena River, Siberia. 2, 5, sample PIN B 70/25, Pestrotsvet Formation, Atdabanian; Oi-Muraan, Lena River, Siberia. 1, longitudinal section showing tufted branched form of thallus, ×75. 2, transverse and oblique sections showing hollow interior of tube, ×75. 3, longitudinal section of individual branched tuft, ×85. 4, detail of 3 showing tubiform nature of filaments, ×215. 5, longitudinal, oblique, and transverse sections of filaments showing the variable preservation of the tubiform morphology, ×75. 6, longitudinal section showing micritic microstructure of skeleton; note how tubes become obscure upwards, ×190. All are uncovered thin sections.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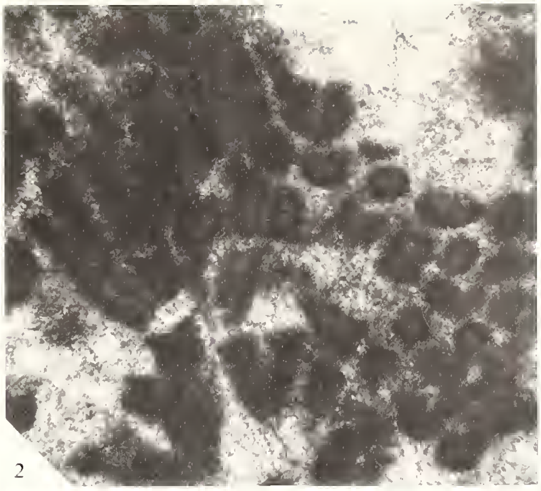
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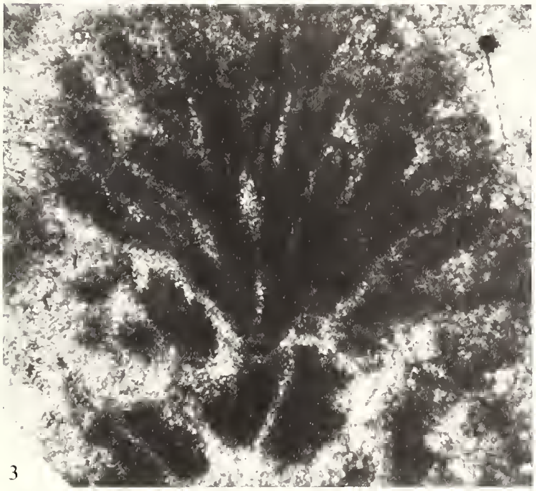
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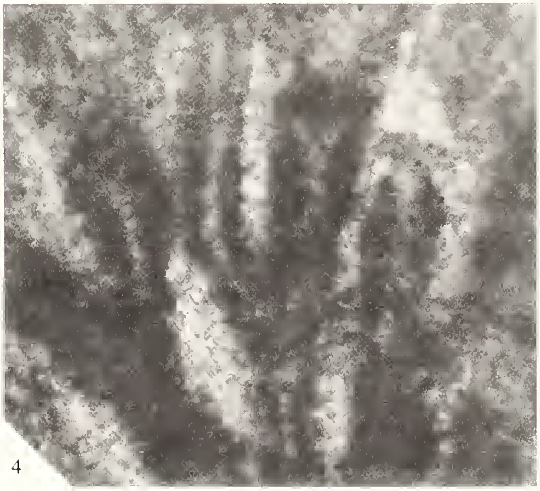
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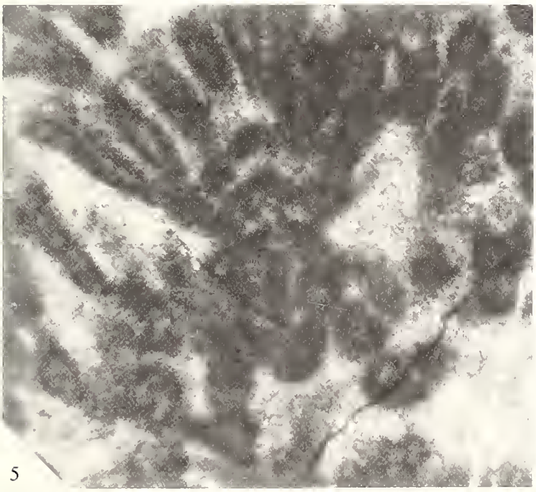
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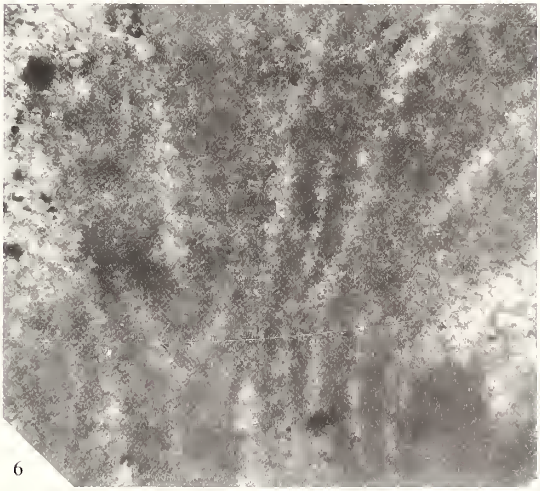
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RIDING and VORONOVA, *Tubomorphophyton*

DISCUSSION

Morphology

Korde (1973) considered *Tubomorphophyton* to be composed of a series of filaments, the 'wall' consisting of filaments more densely packed than those near the centre. In this she believed it to differ from *Epiphyton*, consisting throughout of densely packed filaments, and from *Gordonophyton* whose stacked branches she interpreted as reflecting alternating layers of vertically (light) and horizontally (dark) arranged filaments. We cannot confirm the presence of minute filaments within *Tubomorphophyton* and have only observed uniform micrite in the walls of the tube without any indication of distinctive ultrastructural features.

The tube diameter of *Tubomorphophyton* is comparable to, or slightly greater, than that of porostromates such as *Girvanella* Nicholson and Etheridge and *Ortonella* Garwood, but its wall is normally considerably thicker. In the *Tubomorphophyton* described here the ratio of total wall thickness to tube diameter is generally of the order of 2:3 compared with 1:2 for *Girvanella* (Riding 1977, p. 38) and in thin section specimens of *Tubomorphophyton* are not always obviously tubiform. We regard this as being primarily a reflection of original sheath thickness relative to filament diameter but both filament orientation in thin section and diagenetic modification of skeletal structure contribute to the clarity or otherwise of this feature.

The regular, abundant production of separate branches in *Tubomorphophyton* is similar to that of other epiphytaceans and distinguishes the group as a whole from unbranched or only very occasionally branched forms (*Girvanella*, *Proaulopora*) on the one hand, and from genera with closely appressed filaments (*Hedstroemia* Rothpletz, *Apophoretella* Elliott) on the other.

Affinity

In common with *Epiphyton* and *Gordonophyton* Korde (1973) recognized terminal sporangia in *Tubomorphophyton* and placed all three genera in the red algae under the Epiphytaceae. Most other recent workers have not expressed any confident or specific suggestions concerning the affinity of the group although Luchinina (1975) compared *Epiphyton* with *Rivularia*.

Morphologically, *Tubomorphophyton* somewhat resembles the extant porphyridiacean red alga *Goniotrichum* and similar comparisons can be made with filamentous chlorophytes. This raises the problem, constantly faced in work on fossil calcareous algae, of the significance to be attached to purely morphological similarities between uncalcified Recent forms and calcareous fossils. No calcified Recent filamentous rhodophytes are known to us; calcareous red algae at the present day comprise relatively complex forms such as Corallinaceae, Squamariaceae, and the chaetangiacean *Galaxaura*. These are marine and rhodophytes are uncommon in freshwater habitats at the present day. If red algae were more widely distributed in freshwater environments it is quite possible that they would calcify in tufa deposits, where carbonate deposition on plants occurs much more readily than in the sea. In such a situation calcareous filaments could be produced which might resemble *Tubomorphophyton*.

So, there are two courses open to us: we can either limit comparisons to only extant *calcareous* forms, or we can open up all the possibilities with the question 'if this soft alga happened to calcify, would it produce a skeleton similar to such-and-such a fossil?' Not only does the first course offer an easier approach, it also has the advantage of providing a more convincing basis for comparison; algal calcification may depend in some cases on environmental controls, but on the whole it is limited to particular groups and it is more plausible to compare fossil calcareous algae with extant calcareous forms than with non-calcareous groups. However, the present is not such a comprehensive key to the past; groups become extinct and habitats may change. In order to take these factors into account it is necessary to consider the second course of action, and to compare extant non-calcified forms with calcareous fossils, while still remembering that this difference does weaken any overall similarities which might otherwise occur.

Filamentous forms exist in a wide range of algal groups: cyanophytes, chlorophytes, rhodophytes, and phaeophytes all have numerous examples of this type of organization. The only way to narrow the field of possibilites is to emphasize the particular features of *Tubomorphophyton*: its small size and distinctive morphology.

The Recent small phaeophycean *Ectocarpus* has filament diameters of the order of 25–70 μm (Cardinal 1964), which places it in the same size range as *Tubomorphophyton*, but it has a main axis with lateral branches and also bears numerous reproductive bodies which might be preserved in fossils.

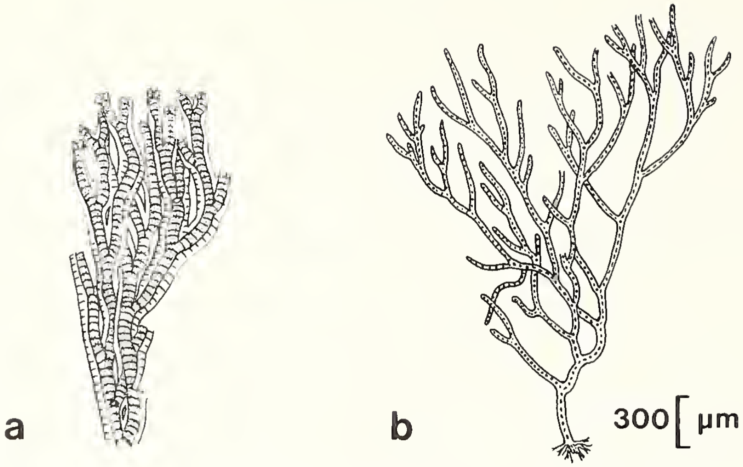
The Nemalionales (Rhodophyta) has a number of small, branched, filamentous forms (see Kylin 1956, pp. 87–88). *Kylinia* is up to about 2 mm high, *Audouinella* is 2–5 mm, and *Acrochaetium* also reaches 5 mm in height. But these genera also have main axes with lateral branches and the overall form does not closely resemble *Tubomorphophyton*.

Tubomorphophyton has a dichotomously branched form, without main axes being developed, and we have seen no spermatangia-like bodies preserved on it. Somewhat closer similarities exist between it and a small cladophoran species, perhaps, than with phaeophytes or rhodophytes. The chlorophyte *Cladophora pygmaea* reaches a height of only 1·0–1·33 mm, even in the adult, and individual filaments are up to 65 μm in diameter (Hoek 1963, pp. 36–37). But even though the gross form of this species resembles that of *Tubomorphophyton*, *C. pygmaea* also tends to show the development of a main axis, and another difference is that the diameter is distinctly variable along a filament (Hoek 1963, pl. 2, fig. 21), which is not the case with *Tubomorphophyton*.

Although none of these examples of eukaryotic algae is known to calcify, it is worth considering whether calcification, if it did occur, would produce a skeleton similar to that of *Tubomorphophyton*. Since *Tubomorphophyton* is a tube, calcification of such eukaryotes would have to be localized on the filament surface: if it were internal it would presumably affect cell walls and produce septa-like cross-partitions of the calcareous tube. Only by being external could it give rise to the simple morphology seen in the fossil. But *Tubomorphophyton* has a limit to its wall thickness, even though it is thick-walled by porostromate standards. The limitation on wall thickness in porostromates such as *Girvanella* and *Ortonella* is imposed by the sheath: it is the sheath which is calcified and sheath-thickness thus determines wall-thickness of the fossil. It is difficult to see how a similar constraint could be imposed on the thickness of an external calcareous layer of *Cladophora*, for example, since there is no distinct sheath present. In fact, calcification of much larger speciments of *Cladophora* has produced tubes in which the wall-thickness is very variable, the tubes, in many cases, being virtually transformed into solid rods (Riding 1979*b*).

But tubiform fossils of the simplicity and size of *Tubomorphophyton* do resemble Recent calcareous cyanophytes in which impregnation by $CaCO_3$ crystals preserved sheath-thickness, diameter, and form (Riding 1977, fig. 1). Sheath character is variable in cyanophytes. In comparison with *Ortonella*, for example, *Tubomorphophyton* has a thicker wall and less clearly tubiform structure, which can be interpreted to reflect a thicker, perhaps more diffluent, sheath. But this does not detract from the comparison between *Tubomorphophyton* and cyanophytes. In fact the wall of *Tubomorphophyton* is relatively thin in proportion to total tube diameter when compared with, say, calcareous *Cladophora*, and this feature of a limitation on wall-thickness indicates that *Tubomorphophyton* was produced by calcification of organic material, such as mucous sheath, with a certain size, rather than by external, unlimited, deposition of $CaCO_3$ on the surface of a filament. This suggests that *Tubomorphophyton* is a cyanophyte and its size, between 20 and 90 μm, is also directly comparable with the external diameter of many cyanophyte sheaths. However, *Tubomorphophyton*'s repeatedly branched thallus with its dichotomous bifurcations is complex by cyanophyte standards. Nevertheless, a few genera do show this type of organization: the stigonemataleans *Loriella* and *Stauromatonema* show erect filaments with forked branching (Fritsch 1959, p. 848). *Stauromatonema* and some genera of the Pulvinulariaceae are markedly heterotrichous (showing prostrate system giving rise to erect growths), but *Loriella* (Fritsch 1959, fig. 328H) appears to be entirely erect and closely resembles *Tubomorphophyton* in form (text-fig. 3*a*).

However, another candidate for comparison is the porphyridiacean (bangialean) rhodophyte *Goniotrichum*. This is a minute branching epiphyte in which some species, e.g. *G. cornu-cervi*, are only up to 1 mm in height. *G. elegans* is taller, but the filaments are only up to 50 μm thick (Newton 1931,



TEXT-FIG. 3. *a*, *Loriella osteophila* Borzi (cyanophyte), size uncertain, from Fritsch (1959, fig. 328*h*), after Borzi. *b*, *Goniotrichum elegans* Le Jolis (rhodophyte) from Newton (1931, fig. 150*b*). The repeated forked branching of *Loriella* more closely resembles *Tubomorphophyton* than does the pseudo-dichotomous branching of *Goniotrichum*.

p. 246). The walls are thick and mucilaginous (Fritsch 1959, p. 427, fig. 143). The dimensions and general form of *Goniotrichum* are comparable with *Tubomorphophyton*, but *Goniotrichum* is described as being pseudo-dichotomously branched (Newton 1931, p. 246) and in detail its thallus does not closely resemble *Tubomorphophyton* (text-fig. 3*b*). Another difference is that extant bangialeans do not calcify, although the mucilaginous envelope of *Goniotrichum* could, possibly, provide a site for calcification in certain circumstances.

Korde's (1959) view of *Epiphyton* is that it is a florideophycidean, and so belongs in the same broad group as the Chaetangiaceae and Corallinaceae. Our conclusion is that although *Tubomorphophyton* may be compared in size and gross morphology with a number of extant eukaryotes, including particularly the rhodophyte *Goniotrichum*, in detailed form and style of calcification it can most closely be compared with cyanophytes, especially certain stigonematateans.

This interpretation has to be tentative; there is so much loss of the type of information used routinely by phycologists to establish comparisons between algae that we are reduced to using features which are not usually diagnostic. Although the possibility that *Tubomorphophyton* is a eukaryote, particularly a bangialean rhodophyte, cannot be excluded, the weight of evidence, in terms of size, morphology, and calcification, suggests to us at present that it is more likely to represent a branched, filamentous cyanophyte.

The solid appearance of some other epiphytaceans could mask a filamentous organization, and the recognition here of a likely cyanophyte nature for *Tubomorphophyton* strengthens the need for re-examination of the affinity of the Epiphytaceae as a whole. This is especially important because of the early appearance of these organisms in the skeletal fossil record: whether they represent cyanophytes or rhodophytes, or are a heterogeneous group of look-alike dendritic fossils, is bound to have considerable bearing on our understanding of the diversity and ecology of early Phanerozoic life on carbonate shelves.

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A NEW ARTICULATED THELODONT (AGNATHA) FROM THE EARLY DEVONIAN OF BRITAIN

by SUSAN TURNER

ABSTRACT. A new articulated early Devonian specimen of a thelodont from Britain is described. It is a nikoliviid and is referred to a new species, *Nikolivia milesi*. The scales of this form bear some resemblance to those of *N. oervigi* (Karatajute-Talimaa 1968) and *N. elongata* (Karatajute-Talimaa 1978), and possibly *N.*? ('*Sigurdia*') *heintzae* (Dineley and Loeffler 1976). The presence of a possible pore canal system is noted. No other new characters to help decide the relationship of thelodonts to other agnatha are present. A comparison is made with other articulated thelodonts and a suggestion for the mode of life is given.

IN August 1933 and June 1934 Dr. E. I. White and Mr. H. A. Toombs collected a suite of early Devonian fishes from Wayne Herbert Quarry, near Newton, Herefordshire (fossils housed in the British Museum (Natural History)). From a green siltstone lenticle and contiguous beds they obtained remarkably complete pteraspids (White 1935), several cephalaspids, as yet undescribed, and acanthodians (Miles 1973). In searching the collection for acanthodian remains in 1971 Dr. Roger Miles noticed on the underside of a slab a patch of scales which were not acanthodian. This specimen, which may have been overlooked because it is obvious only under oblique or subdued lighting, was shown to the author, who confirmed that it was a thelodont.

Articulated thelodonts are rare; most of the fifty to sixty thelodont species described are known from isolated scales. Only two articulated specimens (Pl. 97) and a small patch of scales, all of *Turinia pagei*, have been reported from the Lower Devonian of Britain: from Scotland (Traquair 1899; Ørvig 1969) and Gloucestershire (Allen, Halstead (Tarlo) and Turner 1968). From a preliminary examination I suspected that the Wayne Herbert thelodont might also be *T. pagei*, but further study of a cast of the natural mould reveals that it is a new species of *Nikolivia* (Family Nikoliviidae). Descriptions of nikoliviids have hitherto been based on isolated scales from the early Devonian of Europe (Karatajute-Talimaa 1968, 1978; Turner 1973). Articulated material from Canada, referred to *Sigurdia heintzae*, and undetermined scales figured by Dineley and Loeffler (1976, pl. 22, figs. 65, 66) are considered to belong to this family.

SYSTEMATIC PALAEONTOLOGY

Order THELODONTIDA
Family NIKOLIVIIDAE Karatajute-Talimaa, 1978
Genus NIKOLIVIA Karatajute-Talimaa, 1978

Diagnosis. Small to large thelodonts with triangular pectoral flaps flanking a large cephalothorax, and trunk covered with imbricated scales with some areas of non-imbricated scales. More robust and elongate large scales along the leading edge of the pectoral flaps. For detailed diagnosis of the scales see Karatajute-Talimaa (1978, p. 140).

Type species. *Nikolivia oervigi* (Karatajute-Talimaa, 1968).

Other species. *N. balabayi* Karatajute-Talimaa, 1978; *N. elongata* Karatajute-Talimaa, 1978; *N. gutta* Karatajute-Talimaa, 1978; *N.*? *heintzae* (Dineley and Loeffler, 1976); *N.* sp. (*Apalolepis toombsi pars* Turner, 1973).

[Palaeontology, Vol. 25, Part 4, 1982, pp. 879–889, pl. 97.]

Nikolivia milesi sp. nov.

Text-figs. 1–5.

1972 new articulated thelodont; Turner (1972) p. 18.

Derivation of name. In honour of Dr. R. S. Miles, who recognized the type specimen.

Diagnosis. Large thelodont (in excess of 145 mm). Cephalothorax long with slim triangular pectoral flaps, posterior to which body narrows. Scales average length 1·5 mm with thin lanceolate and leaf-like crowns. Body scale crowns with slightly raised, narrow, grooved central ridge with long posterior spur and one-to-three lateral ridges or steps leading to shorter posterior points. Large lanceolate scales, average size 2 mm along leading edge of flaps and at least part of lateral rim of body. These scales flat-topped, some with a side rib. Small areas of long asymmetrical or subrectangular scales, some possibly with pores, part of a sensory-line system. Elliptical bases with pulp cavity reduced to a slit in older scales.

Holotype. Articulated scales, BMNH P. 53902.

Other material. A smaller patch of scales (P. 58216), approximately 85 × 50 mm, is interpreted as a pectoral flap and part of the thorax and abdomen just posterior to the flap. This specimen was on the underside of a slab with *Pteraspis rostrata* (P. 17526I). A patch of articulated scales alongside the holotype of acanthodian *Uraniacanthus spinosus* Miles, 1973 (P. 16609, pl. 11), may also belong to *N. milesi* (only examined from the photograph).

Horizon and locality. Ditton Series, about 66 m above the main 'Psammosteus Limestone', *Pteraspis crouchi* Zone, Early Devonian, Wayne Herbert Quarry, south-west Hereford and Worcester. (N.B. This is an SSSI monitored by the Nature Conservancy Council.)

Description. The type specimen is preserved as a natural mould in fine-grained sediment. The dimensions of the scale area are about 145 mm along the antero-posterior axis by 60 mm across the widest part.

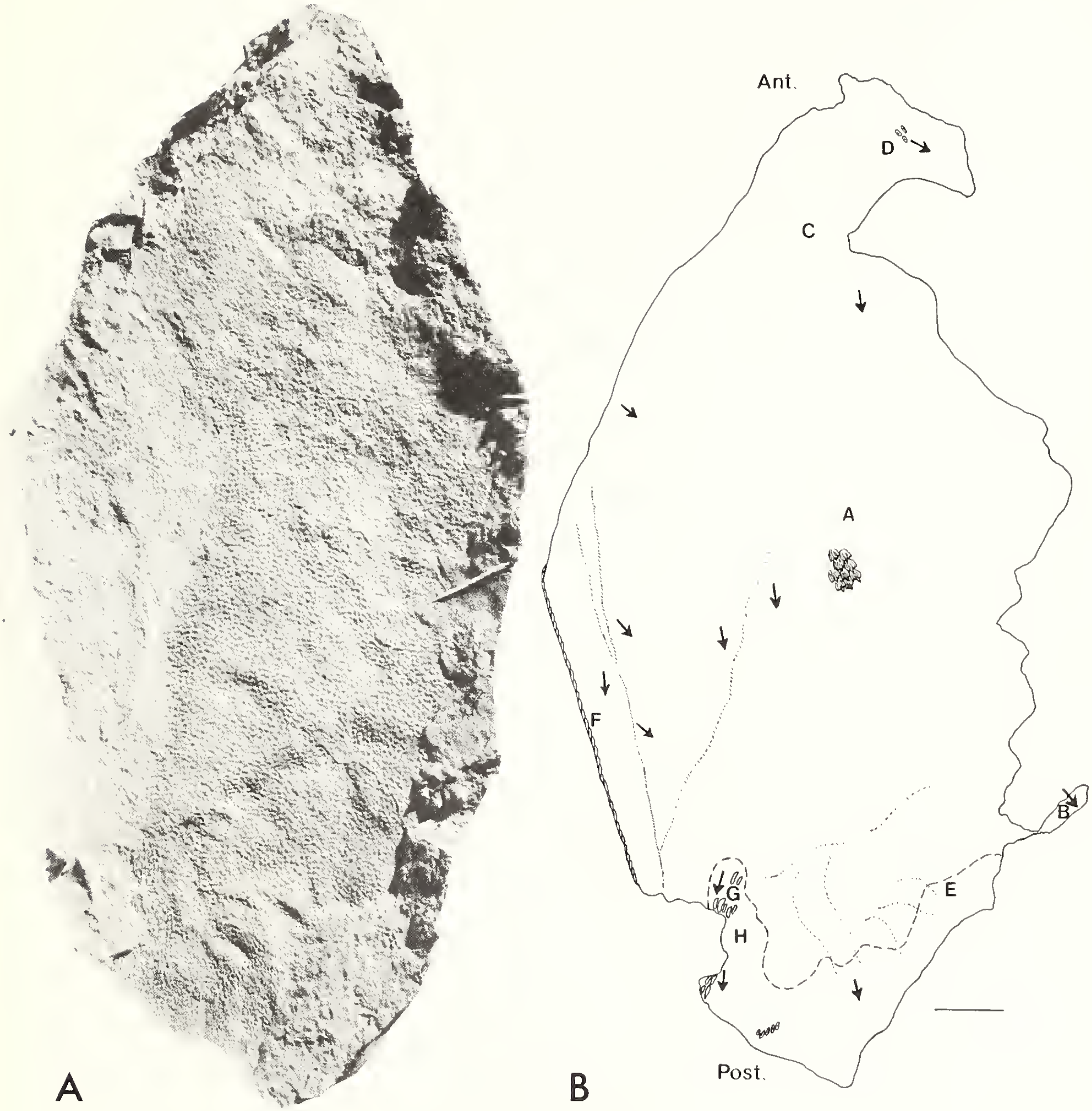
General outline and scale orientation are shown in text-fig. 1. A rough estimate of the scale count in this area is 5000. The only evidence of a natural margin is on the mid-to-lower left side, where the shagreen turns into the rock at about 80°. Here there is a strip of scales the distal edge of which appears to be the rim of the body. This strip tapers posteriorly and ends where the rock is broken (see text-figs. 1, 3). On the inner side of the inturned strip is a marked groove, a fold in the squamation; proximal to this a slight fold passes medially at an angle of about 45°, and fades out anteriorly. There are no other obvious surface features except for shallow ripples.

Over most of the area the typical nikoliviid body scales are partially imbricated, the dentate posterior crown edges just overlapping the anterior edges of the scales behind (see text-figs. 2A, 4). Except for two places the scales are all seen in crown view. Only at the front and in a semicircle near the posterior rim are some preserved base upwards (see text-fig. 1); there they appear to be more lanceolate and possibly not imbricated (text-fig. 2E). On the natural rim the scales can be seen crowded together and in lateral view (text-figs. 2F, 3).

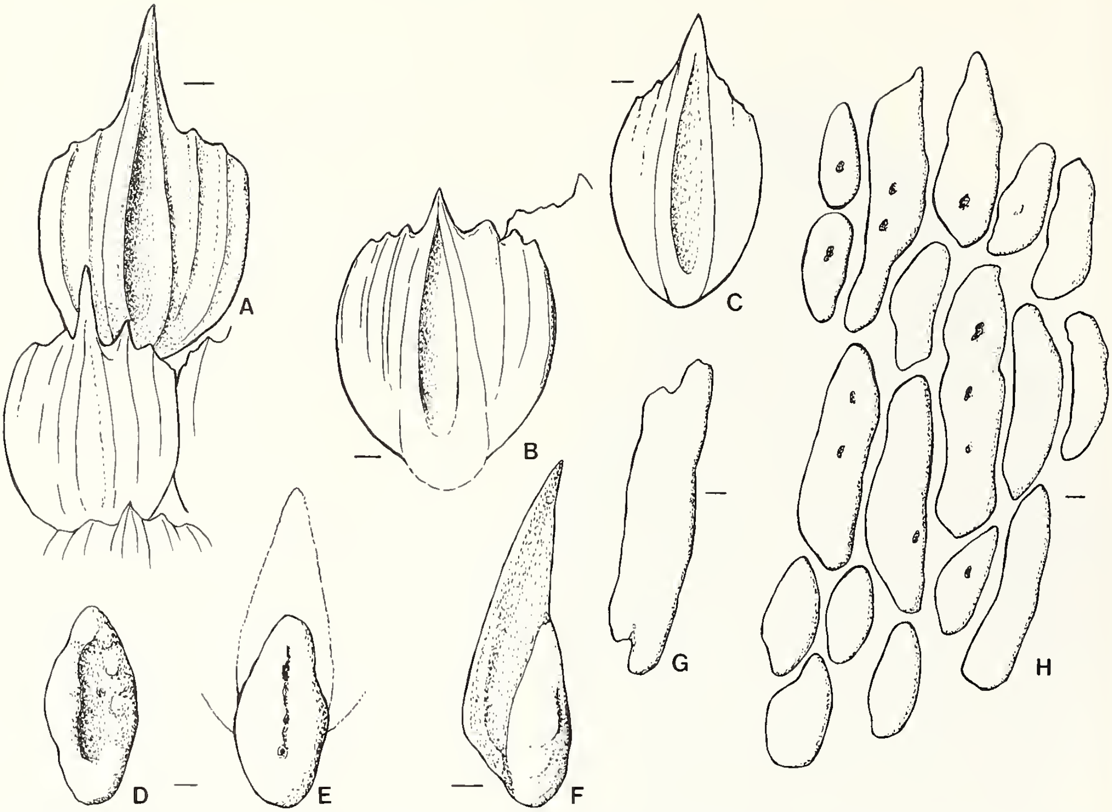
Towards the back on both sides, but clearly on the left, are small areas of atypical scales. These are long, elliptical or subrectangular non-imbricate scales, flanked by typical body scales (see text-figs. 2G, H, 5). In some of these atypical scales there are small depressions or pores which do not appear to be pulp openings (text-fig. 2H). Some of the bases appear to have small thickened nodes around the pulp cavity (text-fig. 2D).

As no scales are preserved other than as impressions no thin section could be made, though from the general form the scales are probably of *Thelodus*-type histology (see Gross 1967) and similar to other nikoliviid scales (see Karatajute-Talimaa 1978).

Discussion. From the evidence of the scale form the Wayne Herbert thelodont is a new species of nikoliviid. Only one scale of *N. oervigi* figured by Karatajute-Talimaa (1978, pl. XLVI, fig. 6*a*) resembles those of *N. milesi*. In fact the crown shapes of this new form look more like those of



TEXT-FIG. 1. *Nikolivia milesi* sp. nov. A, cast of BMNH P. 53902, Early Devonian, Ditton Series, Wayne Herbert Quarry, Hereford and Worcester. B, outline diagram of preserved shagreen. Arrows show scale elongation and anterior to top. Posterior to dashed line most scales appear to be preserved in basal view. Letters mark sites of scales seen in text-figs. 2–5. (Scale line = 1 cm.)



TEXT-FIG. 2. *Nikolivia milesi* sp. nov. A, body scales in crown view showing imbrication. B, body scale in crown view. C, transitional? scale in crown view. D, base of anterior scale. E, base of posterior body scale. F, pectoral flap rim scale in lateral view. G, asymmetrical scale. H, group of asymmetrical scales, showing pores or highly constricted pulp openings. (Scale lines = 0·1 mm.) All from BMNH P. 53902.

Apalolepis; scales of this genus were described by Karatajute-Talimaa (1968, 1978) and Turner (1973). They have a high neck and trumpet-shaped base and differ from nikoliviids with a low-necked base. The scales of *N. milesi* seen in basal and lateral view are similar to those of *N. elongata* and some described as *T.*? *oervigi* by Turner (1973), but unfortunately their crown surfaces are obscured. The scales on the natural margin, however, do appear simpler in outline than the striated body scales (see text-fig. 3).

To date no isolated scales have been extracted from Wayne Herbert rocks, and only a few nikoliviid and apalolepidid scales have been found from other localities in England that could be

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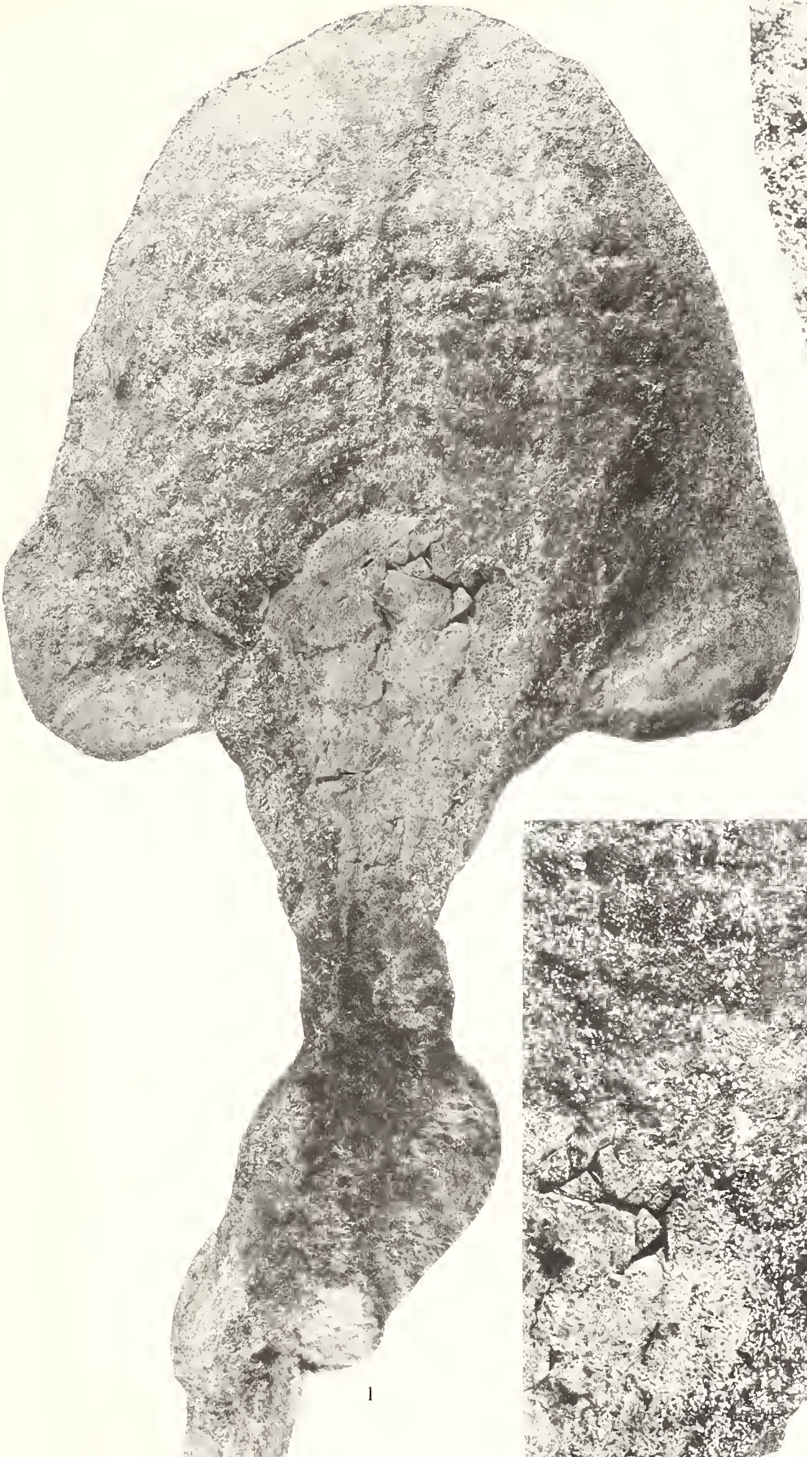
EXPLANATION OF PLATE 97

Figs. 1–3. *Turinia pagei* (Powrie). Holotype (RSM 1891.92.133). Lower Old Red Sandstone, Lower Garvock Group, Turin Hill, Angus, Scotland. 1, whole specimen × $\frac{2}{3}$. 2, branchial and pectoral area to show scale sizes and distribution, × 1 approx. 3, pectoral flap to show scale differentiation and fining of scales on trailing edge, × 1 approx.



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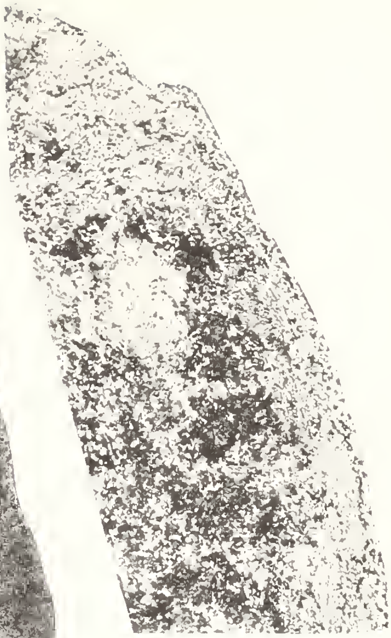

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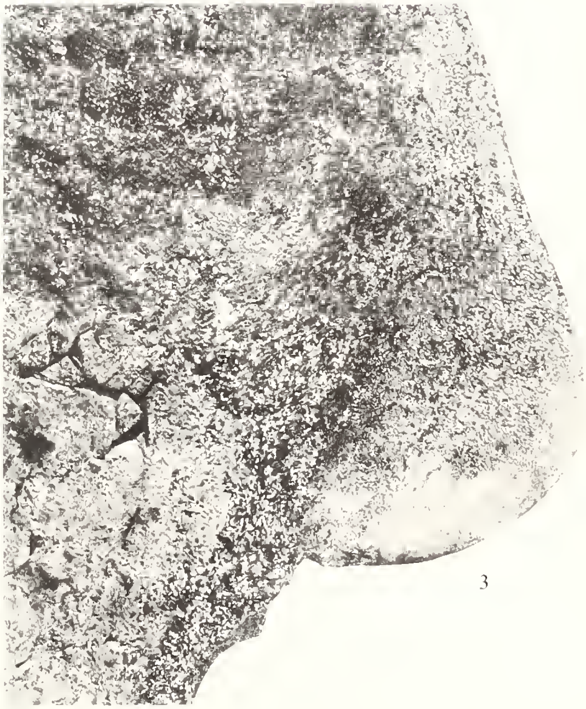


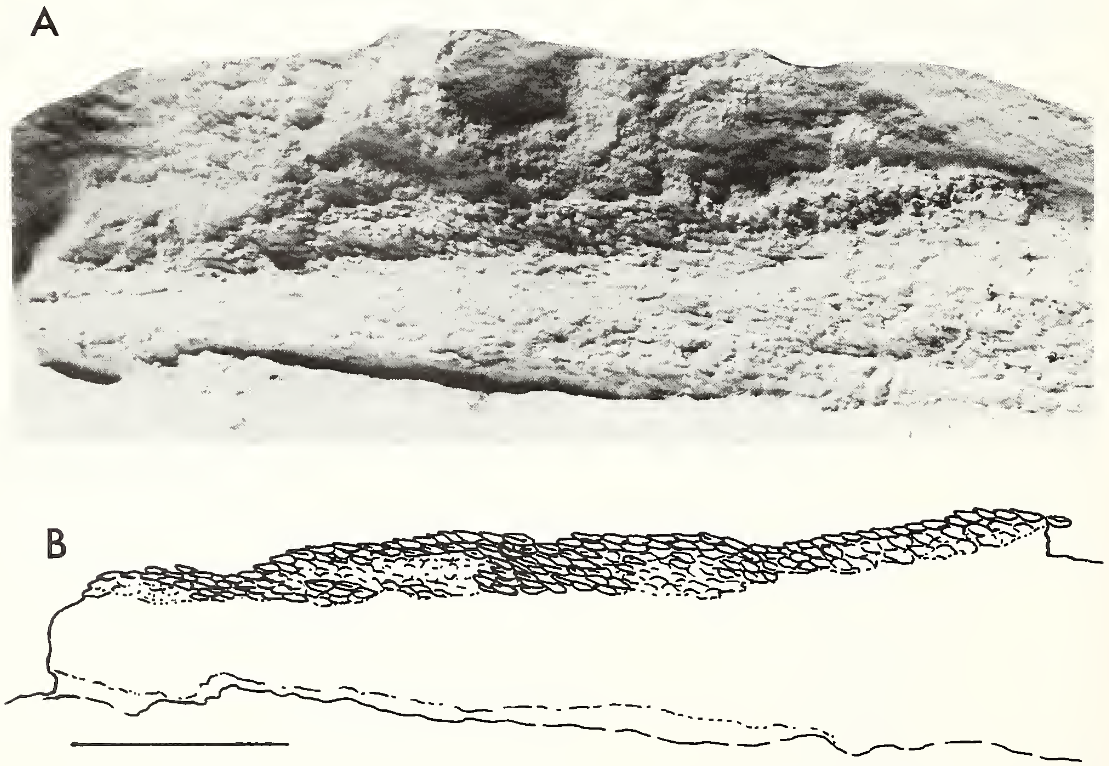
3

TURNER, Early Devonian thelodont

compared with *N. milesi*. Karatajute-Talimaa (1978, p. 129) referred the scales of *A. toombsi* Turner, 1973 to the genus *Nikolivia*. This is accepted in part. However, some of the Welsh Borderland scales are closer to *Apalolepis*, having the high-necked bases, but as so few have yet been found it has not been possible to make a complete histological study. None of the *toombsi* scale forms resemble those of *N. milesi*. The scales of *T.*? *oervigi* from the Welsh Borderland (Turner 1973) fall into the range of *N. oervigi*, *N. elongata*, and *N. balabayi*. It seems feasible that *N. milesi* is closely related to one or more of these, but because of its unusual asymmetrical scale features it is considered to warrant species status.

Comparison with other articulated thelodonts. The pectoral flap does seem to be present in *N. milesi*, preserved as the lateral strip of scales. It is somewhat folded but appears long and narrow, unless the diagonal fold in the main squamation was caused by the rest of the pectoral flap being tucked under during burial. The presence of closely packed, more robust scales on the leading edge of the pectoral fin appears to be a common feature in thelodonts. Usually there are loosely packed, finer and smaller scales on the trailing edge, allowing more flexibility. This is well shown in the holotype *Turinia* (Pl. 97, fig. 3); this edge is obscured in *N. milesi*.

Another thelodont, called *S. heintzae* by Dineley and Loeffler (1976) has large scales along the pectoral flap and also apparently along the body margin as seen flattened dorso-ventrally. Closer examination of these Canadian specimens being undertaken by Dr. Loeffler, Dr. Goujet, and myself confirms that this is a nikoliviid with very similar scale morphology to, although a smaller form than, *N. milesi*. The use of the genus-name *Sigurdia* (Heintz 1972), based as it was upon an impression in



TEXT-FIG. 3. *Nikolivia milesi* sp. nov. A, strip of scales thought to represent the pectoral fin, ×3 approx. B, diagram of strip to show crowded rim scales at site F. (Scale line = 1 cm.)

sandstone from Spitsbergen and thought to be thelodont, despite the lack of scales, should be discontinued.

N. milesi also has structures in common with *Phlebolepis elegans* Pander (see e.g. Ritchie 1968). *Phlebolepis* has a dermal armour of thin, imbricated, ribbed scales, with asymmetrical scales in special areas, and pores through certain scales. This last feature Gross (1968) interpreted as a sensory-line system. The presence of pores in the elongate scales of *N. milesi* may indicate that it too possessed such a system. The region of pore scales, just posterior to the lateral flap, is comparable to that in *P. elegans* (Märss 1979). The similarities between the Silurian *Phlebolepis* and *Nikolivia* do not necessarily signify close relationship because the two forms have scales of different histological structure, *Phlebolepis* being of *Katoporus* type (Gross 1967), although the significance of this dichotomy in thelodont scale structure for phylogenetic relationships is not yet understood.

The criteria for deciding the 'way up' in articulated thelodonts are few. The studies of Kiaer and Heintz (1932) and Ritchie (1963, 1968) have shown that thelodonts had a dorsal and an anal fin and a reversed heterocercal or hypocercal tail; these are helpful indicators if preserved. However, in the absence of these fins it is not easy to be definite. If the specimen of *N. milesi* is structurally on the lower side of the rock then the ventral surface is uppermost. Scales are seen in dorsal (crown) and ventral (basal) view on the same plane, a common occurrence in thelodonts flattened dorso-ventrally. This can be seen in articulated *T. pagei* specimens in the areas where there is no infilling by sediment.

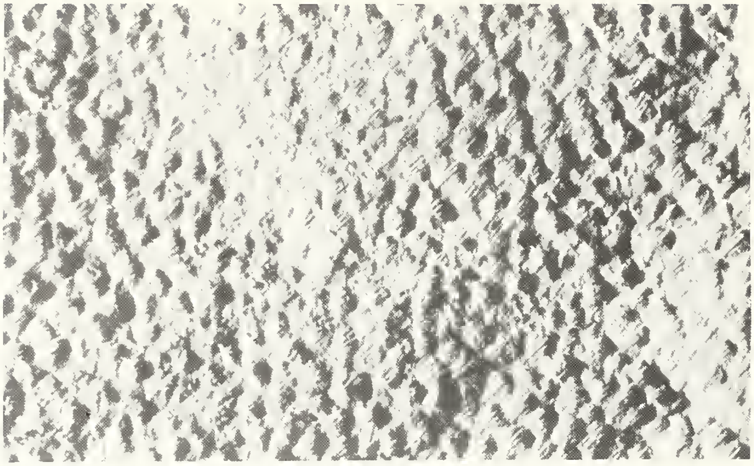
Traquair (1899, p. 599) thought the holotype *Turinia* was in dorsal view because it was 'conclusively shown by the position of the lower lobe of the heterocercal caudal fin'. If all thelodonts have a hypocercal tail, as seems possible from Ritchie's studies, then Traquair's statement is not upheld (see also Kemna 1903). Stensiö (1958, 1964) interpreted *T. pagei* as a heterostracan shown in dorsal view with nine pairs of branchial arches and extrabranchial atria, and impressions of the brain. His separation of *Turinia* from other thelodonts, particularly the family Thelodontidae, is not warranted as *T. pagei* scales are certainly no different histologically from those of the *Thelodus* group, as shown by Gross (1967). *T. pagei* has a general morphology in common with all articulated thelodonts; large cephalothorax with lateral triangular pectoral flaps, slim trunk, and armour of discrete dermal denticles. The lack of distinct orbits and nasal sacs, and the presence of what appears to be the gut region just ventral to the cephalothorax, suggest that the holotype is preserved in ventral view, as first suggested by Powrie (1870). Study of the holotype indicates only seven or eight 'branchial' arches and there is a buccal region leading from the anterior mouth into the pharynx and gut (see Pl. 97, fig. 1).

The area of the body preserved in *N. milesi* appears to coincide with that in the English *Turinia*, i.e. the ventral surface of the cephalothorax (see Allen *et al.* 1968, fig. 3), though there are no obvious branchial structures to be seen. Comparing the pectoral fin size with total length in the type *Turinia* an estimate for the length of *N. milesi* can be given as 205 mm.

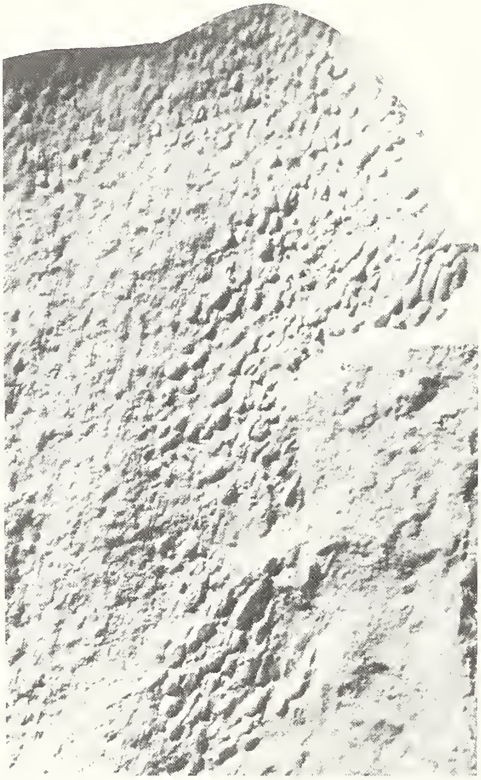
In the type *Turinia* there are small patches of tiny scales distal to the branchial ridges where pectoral flap meets trunk, which may represent flaps covering branchial openings, similar to those postulated for the Scottish Silurian thelodonts (Ritchie 1968). This region is obscured by the infold and scale imbrication in *N. milesi*.

Associated Fauna

Heterostracans	*Pteraspis rostrata* var. *toombsi* *P. rostrata* var. *waynensis* *P. rostrata* var. *virgoi* *P. jackana* *Poraspis sericea* *Weigeltaspis*
Osteostracans	Several species of cephalaspids, including *Cephalaspis jacki*
Acanthodians	Climatiids: *Ptomacanthus anglicus*, *Vernicomacanthus waynensis* Ischnacanthid: *Uraniacanthus spinosus*
Eurypterida	*Pterygotus anglicus*?



TEXT-FIG. 4. *Nikolivia milesi* sp. nov. Body scales from site A to show imbrication of crown tips. Anterior to top right, ×60 approx.



TEXT-FIG. 5. *Nikolivia milesi* sp. nov. Asymmetrical scales from sites G and H. Posterior to top, ×60 approx.

Palaeoenvironment. All the Wayne Herbert fossils came from a green siltstone lenticle or the fine siltstone beds a few inches just above and below (H. A. Toombs, pers. comm. 1981). White (1935, p. 383) interpreted the lenticle, 50 mm thick and covering an area about 3·0 mm × 1·2 m, as a single dried-up pool in which the animals were strictly contemporaneous; Miles (1973, p. 115) agreed that these fluvial species were trapped by the drying up of the body of water in which they lived. Allen and Tarlo (1963) thought a cut-off channel had dried out. The presence of a partially complete thelodont verifies the rapid nature of the event, for presumably, unless buried quickly, thelodonts disintegrated rapidly after death, releasing thousands of scales into the surrounds. The way the pectoral flap is folded suggests it was pressed down into soft bottom sediment, which may indicate the fish were trapped in wet mud. No sedimentary structures of complete drying out have been described, and the fish, although a little disarticulated, are not contorted.

The similarities between *N. milesi*, *Phlebolepis elegans*, an inhabitant of quiet lagoons (Märss and Einasto 1978), and *N.? heintzae*, also interpreted as a quiet lagoonal or hyposaline form (Dineley and Loeffler 1976), suggest that the English form also lived in quiet water, such as the ephemeral ponds and lakes of the early Devonian Welsh Borderland floodplain (Allen and Tarlo 1963). The nikoliviids are apparently rare in British samples, whereas *Turinia* scales are common. Does this mean that the more fragile nikoliviid scales behaved differently as sedimentary particles or that the fish preferred different environments, *Turinia* perhaps being more adapted to bottom living in faster-flowing rivers and streams?

There are at least two large predators in the fauna, the acanthodians, one of which had apparently swallowed or was in the process of swallowing a small cephalaspid (Miles 1973, pl. 1, fig. 2), and eurypterids, both of which may have regarded thelodonts as prey.

Stratigraphical significance. The nikoliviids now seem to be an integral part of the early Devonian thelodont fauna in Europe. They are found often in association with turiniids (Karatajute-Talimaa 1978; Turner 1973). The presence of nikoliviids in North-West Canada in rocks of Late Silurian or early Devonian age (Dineley and Loeffler 1976; Vieth 1980) also indicates the close links between North America and Europe at this time. Recently they have been found in younger Devonian rocks in Australia associated with turiniids (Turner and Dring 1981; Turner, Jones and Draper 1981).

Geographical and stratigraphical range of nikoliviids

UK ENGLAND	Herefordshire	*Nikolivia milesi*	Middle Dittonian
	Welsh Borderland (Mainly Brown Clee area, Turner 1973)	*N.* cf. *balabayi* *N.* cf. *elongata* *N. oervigi* *N. toombsi*	Lower to middle Dittonian
USSR (Karatajute-Talimaa, 1978)	Lithuania	*N. balabayi*? *N. elongata*	Middle Dittonian
	Latvia	*N. balabayi* *N. elongata*	Middle Dittonian
	Estonia	*N. gutta* *N. elongata*	Lower Dittonian
	Brest	*N. gutta* *N. elongata*	Lower Dittonian
	Volini	*N. elongata*	Lower Dittonian
	Podolia	*N. oervigi* *N. elongata*	Middle Dittonian
		N. balabayi *N. elongata*	Lower Dittonian

[*Table continued overleaf*]

Geographical and stratigraphical range of nikoliviids (cont.)

CANADA	Mackenzie Mountains, North West Territories (Dineley and Loeffler 1976)	*N.? heintzae*	Transitional, between Delorme Fm. and Road River Fm. Lower Dittonian?
	Canadian Arctic (Vieth 1980)	nikoliviids, including *Canonia grossi*	Lower Devonian
SPITSBERGEN	Dr. Daniel Goujet (pers. comm.)	*Nikolivia* spp.	Lower Devonian
AUSTRALIA	Carnarvon Basin (Turner and Dring 1981) Toko Syncline (Turner *et al.* 1981)	nikoliviid indet.	Lower to Upper Devonian

Abbreviations:		
	BMNH P.	British Museum (Natural History), Department of Palaeontology
	RSM	Royal Scottish Museum, Edinburgh
	BU	Birmingham University

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TOOTH STRUCTURE OF THE PYGASTEROID SEA URCHIN *PLESIECHINUS*

by ANDREW B. SMITH

ABSTRACT. The fine structure of a tooth thought to belong to the Jurassic pygasteroid *Plesiechinus ornatus* (Buckman) is described and the tooth elements are reconstructed. The tooth is quite distinct from contemporary and Recent keeled teeth of regular echinoids but has a structure similar to that of known teeth of irregular echinoids. The discovery that pygasteroids have teeth constructed like other irregular echinoid teeth so far described strengthens the view that irregular echinoids are a monophyletic group.

PYGASTEROIDS have long been recognized as primitive irregular echinoids, but the exact relationship of pygasteroids to the other irregular echinoids has, however, been disputed. Early workers considered pygasteroids and holectypoids to be closely related and for many years the family Pygasteridae was classified within the Holectypoida. The first serious attack on this view was made by Mortensen (1948), who considered that pygasteroids arose independently from other holectypoids. This view was accepted by Durham and Melville (1957), who erected the order Pygasteroida to accommodate them, principally on the assumption that pygasteroids would prove to have grooved teeth in contrast to the 'keeled' teeth they had described in *Holectypus.*

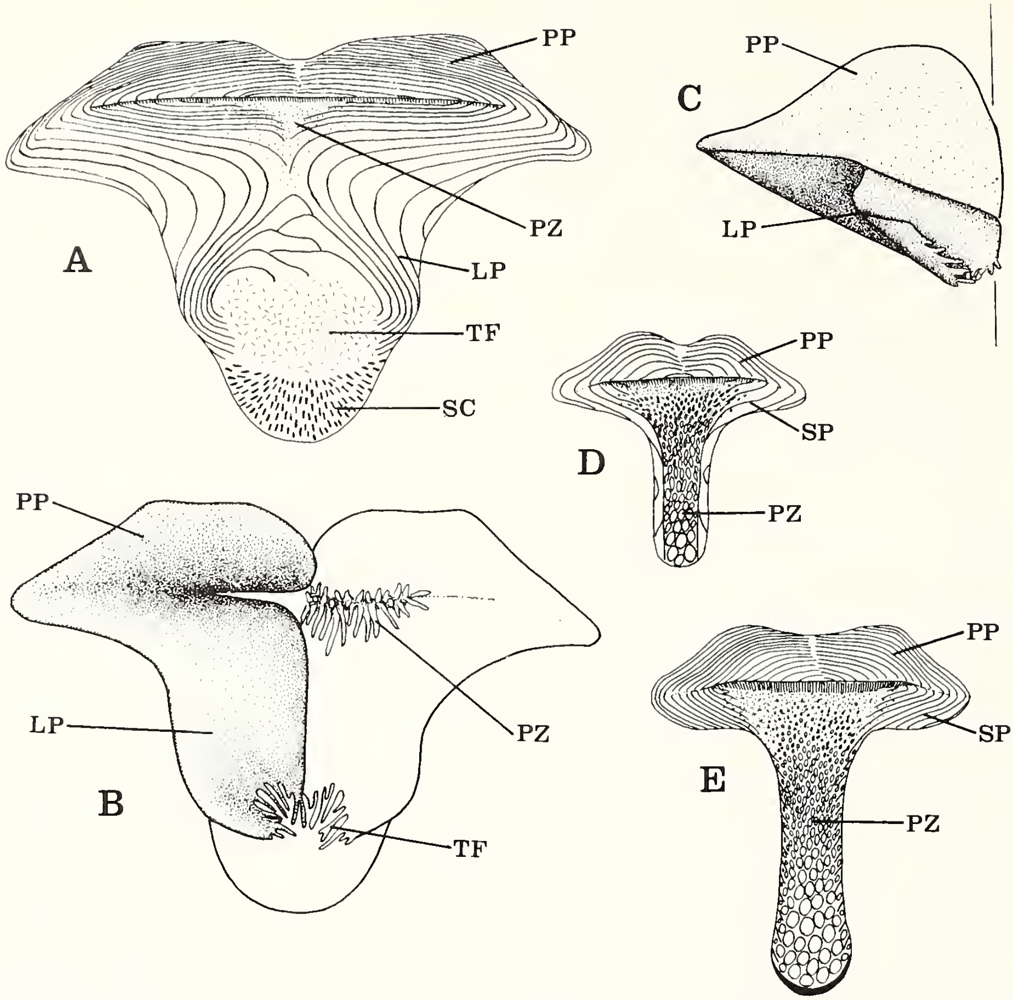
In 1961 Melville published the first description of a pygasteroid lantern. He showed that *Pygaster trigeri* Cotteau had stout, triangular teeth and pyramids with a very deep V-shaped foramen magnum. Melville argued that the unique shape of pygasteroid teeth proved that pygasteroids were unrelated to other irregular echinoids. However, Melville had apparently overlooked Hawkins's (1909) work on holectypoid teeth, where stout, diamond-shaped teeth were illustrated, and based his argument on a misinterpretation of the teeth of *Holectypus.* Critical re-examination of the specimen of *Holectypus*, from which Durham and Melville (1957) described and illustrated teeth, has shown that the teeth are stout and triangular in cross-section rather than keeled (Kier 1974; Smith 1981) and similar observations on another specimen have been made by Hess (1971). I have recently argued that Pygasteroids and Holectypoids are sister groups and form a monophyletic group Eognathostomata (Smith 1981).

The purpose of this paper is to describe the ultrastructure of teeth thought to belong to the pygasteroid *Plesiechinus ornatus* (Buckman) from the Lower Bajocian (Middle Jurassic) of the Cotswolds. This allows critical comparison to be made with tooth structure in other groups of echinoid, since Melville's original material is not available for SEM study.

Methods and materials

The Pea Grit (Crickley Oncolite lithofacies of Mudge 1978) is a horizon famed for its fossil echinoid fauna. It belongs to the *murchisonae* Zone of the Bajocian, Middle Jurassic, and over the years bed-by-bed collections of the echinoid fauna have been made. Sievings taken from a marly horizon in the Crickley Oncolite at Crickley Hill, near Cheltenham by Dr. C. R. C. Paul proved to contain quantities of lantern elements. Collection from this unit has yielded some 200 specimens of echinoid. *P. ornatus* (Buckman) is the commonest species, making up 42% of the echinoid fauna. The echinaceans *Trochotiara depressus* (Agassiz) (31%), *Acrosalenia lycetti* Wright (10%), and *Psephechinus deslongchampsi* (Wright) (4%) are also important. The rest of the fauna is composed of echinoids with grooved teeth—the pedinoid *Hemipedina perforata* Wright (6%) and cidarids (5%)—together with the irregular *Galeropygus agariciformis* (Forbes) (2%) that has no lantern.

[Palaeontology, Vol. 25, Part 4, 1982, pp. 891–896, pl. 98.]



TEXT-FIG. 1. A–C, tooth of *Plesiechinus* (BMNH E 76938). A, cross-section, slightly restored from Plate 98, fig. 1. B, C, reconstruction of a single tooth element: B, apical view showing left-hand element in detail (prisms restored in only the right-hand element for clarity); C, adaxial view of left-hand element—vertical line marks the mid-line of the tooth. D, cross-section of a keeled tooth from an unknown echinacean collected from the Pea Grit of Crickley Hill, Cotswolds (Bajocian) (BMNH E 76940). E, cross-section of the tooth of *Acrosalenia pustulosa* from the White Limestone (Bathonian) at Northbrook Farm, Oxfordshire. (BMNH E 76939). LP = lateral plate; PP = primary plate; PZ = prism zone; SC = secondary calcite crust; SP = secondary plate; TF = terminal fibres.

EXPLANATION OF PLATE 98

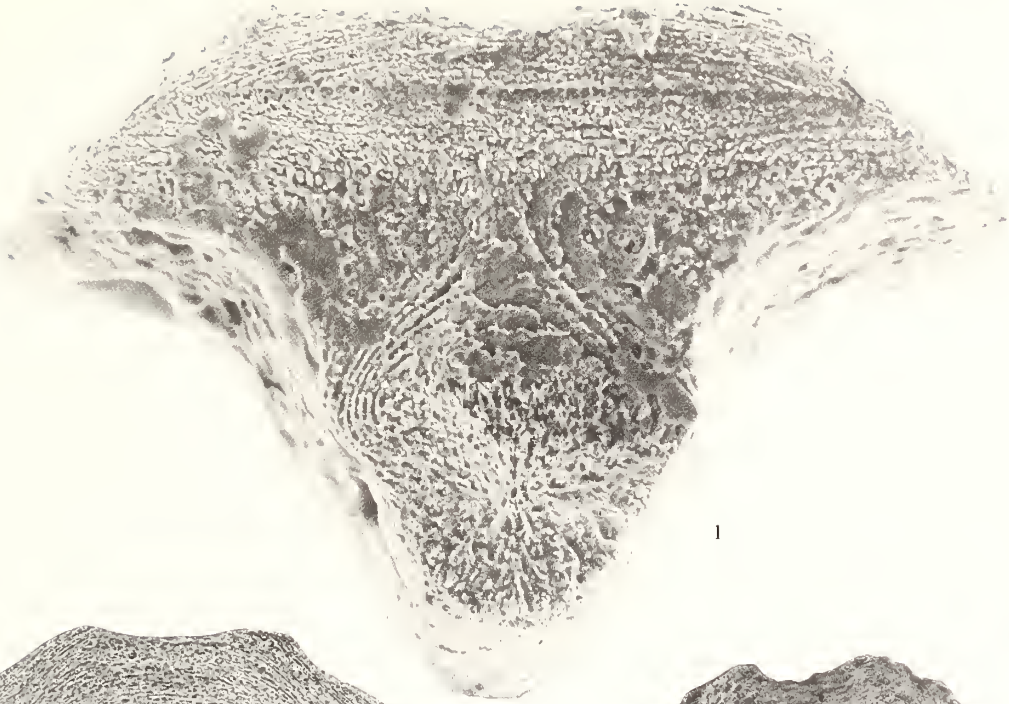
Figs. 1–3. Tooth of *Plesiechinus ornatus* (Buckman). 1, cross-section, abaxial edge to the top, × 200. 2, oblique view of adaxial face, × 60. 3, adaxial face, × 120. BMNH E 76938.

Fig. 4. Tooth of *Acrosalenia pustulosa* Forbes, cross-section, abaxial edge to the top, × 100. BMNH E 76939.

Fig. 5. Keeled tooth of an unknown echinacean in cross-section, abaxial adge to the top, × 100. BMNH E 76940.

All figures are SEM photomicrographs (details of specimens in text-fig. 1).

PLATE 98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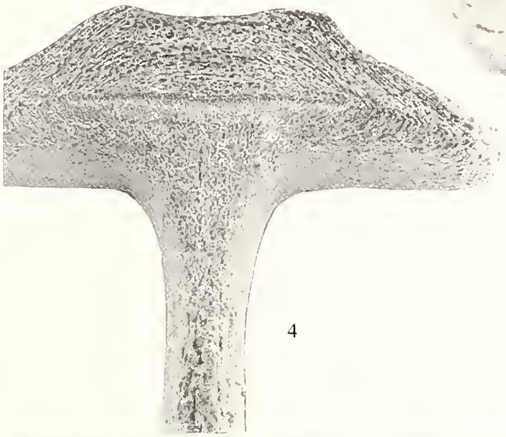
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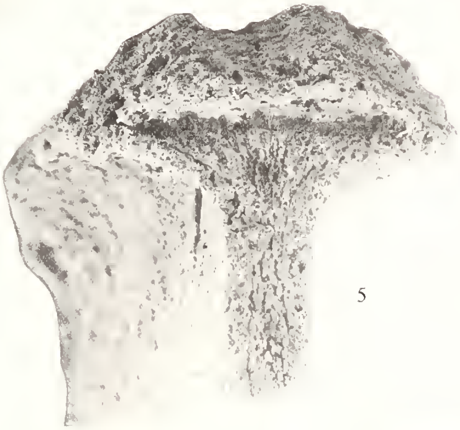
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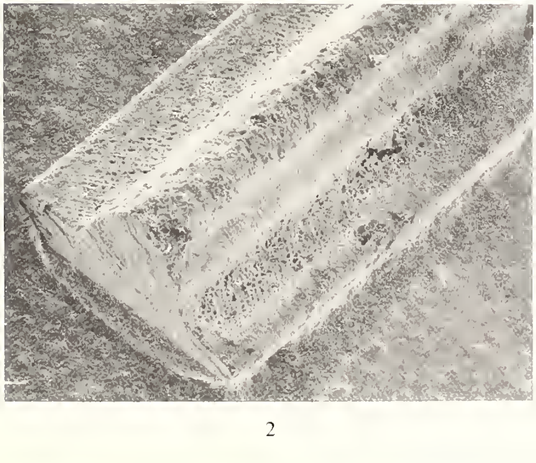
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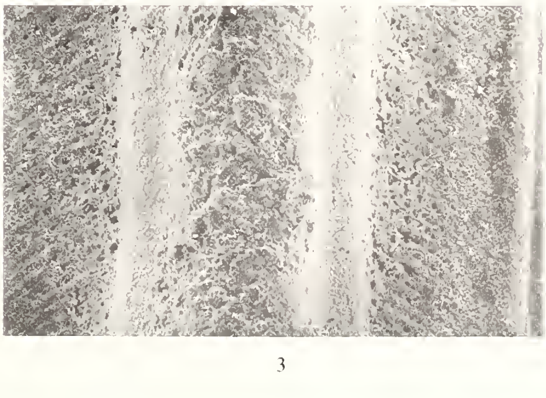
3

SMITH, echinoid teeth

Amongst several typically echinacean (keeled) teeth one different tooth of large size and distinctive shape was found. Although it is impossible to prove just which species these lantern elements come from, it seems fairly certain that the large and distinctive tooth belongs to *Plesiechinus. Plesiechinus* grows to three or four times the size of any of the regular echinoids and its teeth will be correspondingly larger. More importantly, the tooth described here is identical in shape to the tooth described by Melville (1961) from a pygasteroid. Only pygasteroids and holectypoids are known to have teeth of this shape and no holectypoid has ever been collected from these beds.

Echinoid teeth were etched in E.D.T.A. (ethylene diamine tetracetic acid) for about one hour in order to develop the stereom microstructure. This had little effect on the tooth of *Plesiechinus* which was then etched for twenty seconds in 10% HCl to reveal stereom. Specimens were mounted and gold-coated for the SEM. All specimens are now in the collections of the British Museum (Natural History).

ULTRASTRUCTURE OF THE TOOTH OF *PLESIECHINUS*

The tooth, which lacks both the aboral plumula and the oral chewing edge, is more or less straight. The abaxial face is broad and relatively flat with a marked median groove. The axial face has a stout, triangular process with a clear convex ridge on either side and a smoothly-rounded adaxial edge (Pl. 98, figs. 2, 3). Obliquely-running plates can be seen on either side of the stout process as well as on the abaxial face.

In cross-section, the tooth has a very distinctive outline (text-fig. 1A). Like all teeth of post-Palaeozoic echinoids, it is composed of two vertical series of plates that overlap slightly along the mid-line. The primary tooth plates lie abaxially and are steeply inclined. Lateral plates, which are adaxial extensions of the primary plates, make up most of the tooth. They are folded and set obliquely so that, in cross-section, they appear as S-shaped lines (Pl. 98, fig. 1; text-fig. 1A). The two series of lateral plates overlap and this zone of overlap becomes more pronounced adaxially towards their free end. The line separating primary and lateral plates is well marked across most of the tooth. The prism zone is poorly differentiated. Small prisms can be seen between the lateral plates centrally but no distinct zone of prismatic stereom is developed. The adaxial edge is smoothly rounded and, in cross-section, consists of dense, radially aligned stereom. Lateral plates do not extend into this area. By comparison with teeth of other echinoids, this is interpreted as a secondary calcite thickening, probably composed of polycrystalline calcite. Similar radial crusts have been reported in the teeth of diadematoids (Märkel 1970*a*). Beneath this adaxial crust is a zone of fine fibrous stereom interpreted as an area of terminal fibres extending from the free ends of lateral plates. The position of this zone distal to the primary plates and enclosed by the abaxial ends of the lateral plates shows it has nothing to do with the prism zone. Distal splitting of lateral plates producing fine terminal fibres is known to occur in several irregular echinoids (see Märkel 1978, fig. 10*a*; Jensen 1979, fig. 3).

An attempt at reconstructing the shape of tooth plates of *Plesiechinus* from the cross-section is given in text-fig. 1B, C.

COMPARISON WITH OTHER TEETH

The structure of the tooth described above is fundamentally different from any keeled tooth known from regular echinoids. The ultrastructure of keeled teeth of Recent regular echinoids has been reviewed by Märkel (1969) and, for comparison, the ultrastructure of keeled teeth of the Bathonian echinacean *Acrosalenia pustulosa* Forbes and an unknown echinacean tooth from the Pea Grit are illustrated (Pl. 98, figs. 4, 5; text-fig. 1D, E). These teeth have a sharp, narrow keel formed largely of prismatic stereom. Narrow side plates are attached to the distal parts of the primary plates. They are elongate and usually form a narrow margin to the keel. The extension of the secondary plate along the keel is termed the carinal appendage. This may form an almost flat and clearly defined margin (text-fig. 1D; Pl. 98, fig. 5) or may be highly curved and almost totally obliterated by prismatic stereom (text-fig. 1E; Pl. 98, fig. 4). Individual prisms become larger adaxially and at the adaxial edge there is sometimes a thin crust of dense stereom. The supposed pygasteroid tooth is quite evidently unrelated to such keeled teeth.

In structure, pygasteroid teeth come closer to the teeth described from cassiduloids and clypeasteroids (see Märkel, 1970*b*; 1978) and the teeth of *Eodiadema* (see Smith 1981). In *Eodiadema*, cassiduloids, and the more primitive clypeasteroids the prism zone is small and central and the lateral plates overlap along the mid-line and form a broad triangular process. The lateral plates are folded adorally, though folding is usually not quite so developed as it is in pygasteroid teeth. The adaxial splitting of the free end of lateral plates is a feature found only in irregular echinoid teeth and comparable elements were illustrated in fibulariids by Märkel (1978, fig. 10*a*).

Märkel (1978) first pointed out the differences between 'regular type' teeth (i.e. keeled and grooved teeth) and 'clypeasteroid type' teeth (i.e. diamond-shaped or wedge-shaped teeth of irregulars). He distinguished these types on fundamental differences of tooth-element shape. The reconstruction of a pygasteroid tooth element based on the cross-section (text-fig. 1B, C) shows that it undoubtedly belongs to the 'clypeasteroid type'. The adorally folded lateral plate element, the restriction of the prism zone to a small, central region, and the overlap of lateral plate elements along the mid-line are all important features. However, the primary plates are rather larger than in most irregular echinoid teeth, hence the broad abaxial crossbar to the tooth. In this respect the primary tooth elements have some similarity to less elongate primary tooth elements of regular echinoids.

The differences between the supposed pygasteroid tooth on the one hand and teeth of *Eodiadema*, cassiduloids, and primitive clypeasteroids on the other are simply due to size. The pygasteroid tooth probably passed through a diamond-shaped stage in its growth. The structure of pygasteroid teeth represents modification and expansion of the simple tooth elements of irregular echinoids.

PHYLOGENETIC IMPLICATIONS

The tooth of pygasteroids is very similar in shape to the tooth of the holectypoid *Holectypus* (see Kier 1974, text-fig. 54; Smith 1981, text-fig. 6). Pygasteroid teeth are constructed like the teeth of other irregular echinoids and the teeth of *Eodiadema*. The minor differences seen simply reflect the large size attained by these teeth and are modifications through growth of the simpler tooth plan seen in *Eodiadema* and cassiduloids. The fact that the holectypoid *Camerogalerus*, which has relatively small teeth, possesses diamond-shaped teeth indistinguishable from the teeth of *Eodiadema* and cassiduloids (Smith 1981) supports the view that the larger tooth of *Holectypus* is a diamond-shaped tooth modified by growth.

The discovery that tooth elements of pygasteroids belong to the irregular type supports the view that all irregular echinoids belong to a monophyletic group as argued previously (Smith 1981). It is also in keeping with the suggestion that pygasteroids and holectypoids are sister groups and should be classified together.

Acknowledgements. I would like to thank Dr. C. R. C. Paul for providing me with the samples of lantern elements from the Pea Grit and Dr. T. Palmer for sending me specimens of *Acrosalenia pustulosa* to excavate for lantern elements. Mr. C. Veltkamp helped with scanning electron microscopy.

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THE FIRST TRUE ANOMIID BIVALVE?

by F. T. FÜRSICH *and* T. J. PALMER

ABSTRACT. A new anomiid, here designated *Eonomia timida* gen. et sp. nov., is described from the Upper Bathonian and Oxfordian (Middle and Upper Jurassic) of England and Normandy. Its attachment to the substrate by pallial secretion, and the detailed structure of its ligamental area, distinguish it from later members of the family. Uncertainty about the taxonomic position of previously described pre-Cretaceous members of the family makes it a likely candidate for the earliest known anomiid.

THE Middle and Upper Jurassic rocks of southern England and Normandy constitute some of the best-known geological sections in the world. Their faunas have been studied and restudied by a succession of eminent palaeontologists and stratigraphers for more than 150 years; hence it was surprising to discover, at a number of different localities and stratigraphic horizons, common and well-preserved individuals of a distinctive species of bivalve mollusc which cannot be placed in any known Recent or fossil genus. The purpose of this paper is to describe the occurence, morphology, ecology, and evolutionary significance of these bivalves. All material is housed in the Oxford University Museum (Nos. OUM J 40184–40199 and OUM JZ 1782–1790).

OCCURRENCE

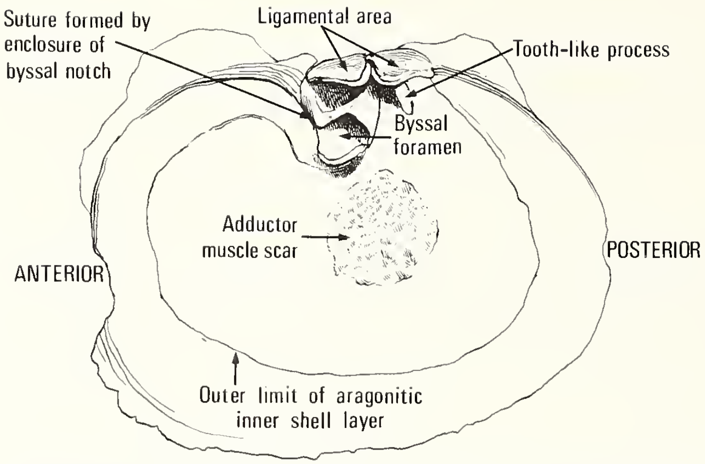
All known specimens of the bivalve here described consist of right valves firmly cemented to hard substrates. These substrates may be of organic origin (oyster shells, sponges, bone) or inorganic origin (hardgrounds). The specimens come from two broad stratigraphic intervals. The first is of Upper Bathonian age and corresponds to the zones of *Oppelia* (*Oxycerites*) *aspidoides* and *Clydoniceras discus*. In Normandy, specimens are common on the roofs of cavities beneath hardgrounds and on the sides of burrows which penetrate hardground surfaces. The hardground which incorporates the top surface of the lithistid sponge reefs at Luc-sur-Mer, Normandy (Fürsich and Palmer 1979) is a particularly good source of material. In England, the roofs of the cavities beneath the Bradford Clay hardground support many examples (Palmer and Fürsich 1974). They were misidentified as *Plicatula* sp. 2 in that account.

The second stratigraphic level which has yielded much material is the upper part of the Oxford Clay and the lower part of the Corallian (*mariae*, *cordatum*, and *plicatilis* Zones). In Normandy, exceptionally well-preserved material comes from the highest of these three zones, in the Argiles à *Lopha gregarea* near the top of the Falaises des Vaches Noires, east of Houlgate. In England, abundant material comes from the Upper Oxford Clay in the Oxford region, where they are found attached to oyster shells and plesiosaur bones. Considering how commonly valves of the new bivalve are found on these substrates in museum collections, it seems surprising that they have not been recognized and described before. Doubtless they occur elsewhere in England and northern France at localities where we have not searched for them.

MORPHOLOGY

The following description, unless otherwise stated, refers to the interior of the right valve (Pl. 99, figs. 1–6; text-fig. 1). Apart from a single specimen from the Oxfordian of Oxfordshire which shows a small fragment of the umbonal region of the left valve still emplaced above the corresponding position in the right valve (Pl. 99, fig. 6), all available material consists of right valves firmly cemented by pallial secretion to hard substrates.

[Palaeontology, Vol. 25, Part 4, 1982, pp. 897–903, pl. 99.]


Suture formed by enclosure of byssal notch
Ligamental area
Tooth-like process
Byssal foramen
Adductor muscle scar
ANTERIOR
POSTERIOR
Outer limit of aragonitic inner shell layer

TEXT-FIG. 1. Line drawing of holotype of *Eonomia timida* gen. et sp. nov. (Pl. 99, fig. 1) showing hard-part morphology of the right valve.

The specimens are circular to subcircular (the length exceeding the height) in plan view, being flat or slightly bowl-shaped in accordance with the contours of the substrate to which they are cemented (Pl. 99, figs. 1, 5, 6). They range up to a height of 8 cm, but most specimens are in the order of 3–5 cm. The Oxfordian examples reach a larger size than those from the Bathonian, which do not exceed a height of 4 cm (Pl. 99, fig. 5). All specimens clearly show a central region formerly covered by a shell layer which has subsequently dissolved away to leave a shallow saucer-shaped depression (Pl. 99, fig. 1). This is inferred to have been the inner aragonitic shell layer, probably of cross-lamellar structure (text-fig. 1). This layer was covered on the outside by a well-developed and conspicuous layer of calcite folia which overlapped the presumed aragonite layer to form the inner face of the valve around the margin. The width of this lunate marginal region tapers to nothing in the dorsal shoulders of the shell, but ventrally reaches 2 cm in the largest examples. It is in turn covered on the outside by a thin (0·2 mm) layer of calcite prisms in some specimens. We have not been able to see this layer in all specimens. The thickness of the combined calcite layers in the ventral region where they account for the total valve thickness ranges from about 1 mm in the smaller specimens to just over 5 mm in a large specimen in which the shell had grown beyond the edge of the hard substrate. In this case, the outer surface of the free-growing part of the shell is seen to be thrown into irregularly concentric projecting rugae formed by the overlapping layers of calcite folia. The similarity of the shell structure of this part of the shell to that of oysters, together with the similar encrusting habit, is probably the main reason why these bivalves have previously been overlooked.

The specimens from the Oxfordian of Normandy are better preserved than any of the others, because traces remain of structures which are inferred originally to have been of aragonite (Pl. 99, figs 1–3). They are preserved

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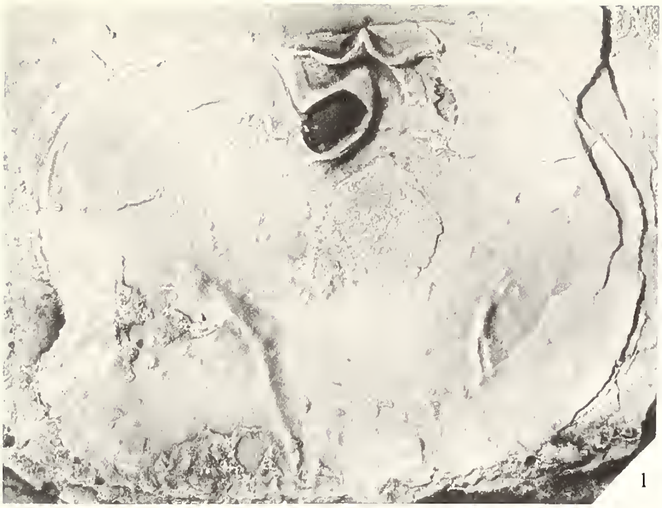
EXPLANATION OF PLATE 99

Figs. 1–6. Right valves of *Eonomia timida* gen. et sp. nov., attached to hard substrates by pallial secretion. 1, general view of holotype, OUM JZ 1782, from the Upper Oxfordian of Normandy, ×2·3. 2, close-up of specimen shown in fig. 1, showing ligamental area with tooth-like process emerging from its posteroventral margin, byssal foramen joined by a suture to the anterodorsal shell margin, and adductor muscle scar, ×4·5. 3, paratype from same locality as holotype showing the thickened and raised edge of the byssal foramen typical of adult specimens. OUM JZ 1783, ×2·2. 4, paratype from Upper Oxford Clay, Stanton Harcourt, Oxfordshire. Specimens from England show no trace of those features of the shell, such as the muscle scar and the ligamental area, which were originally composed of aragonite. OUM J 40195, ×1·8. 5, paratype attached to wall of burrow below hardground, Upper Bathonian, Ranville, Normandy. OUM JZ 1790, ×2·0 6, paratype from Upper Oxford Clay, Stanton Harcourt, Oxfordshire showing a fragment of the left valve still in position above the hinge of the right valve. Its umbo (arrowed) is marginal. OUM J 40199, ×2·2.

PLATE 99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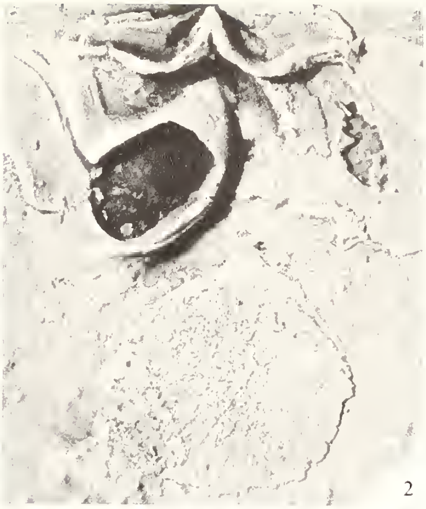
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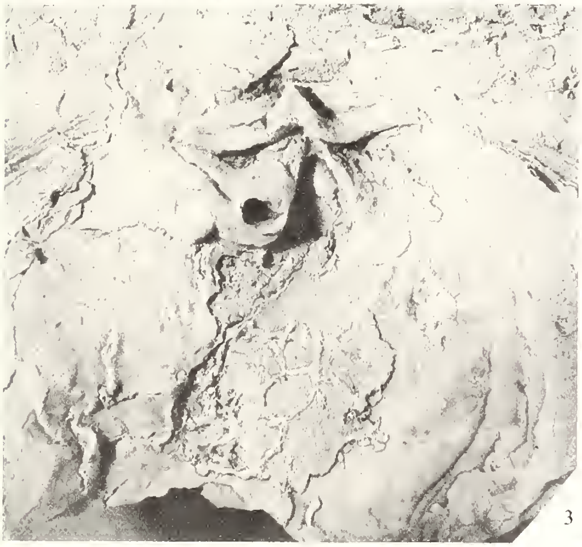
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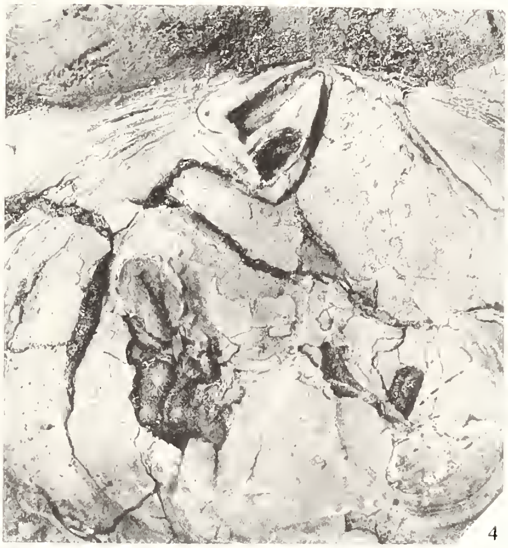
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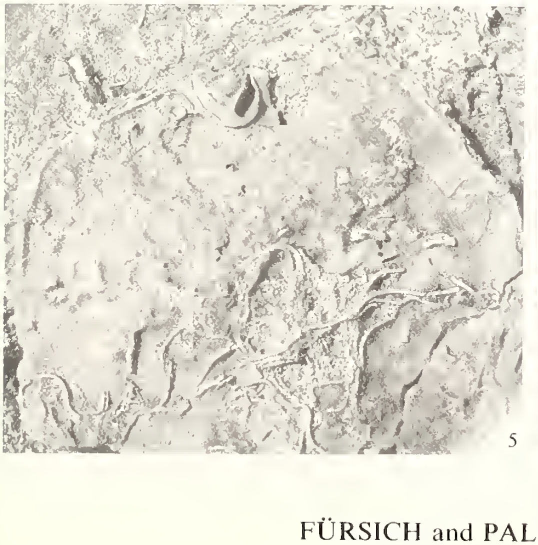
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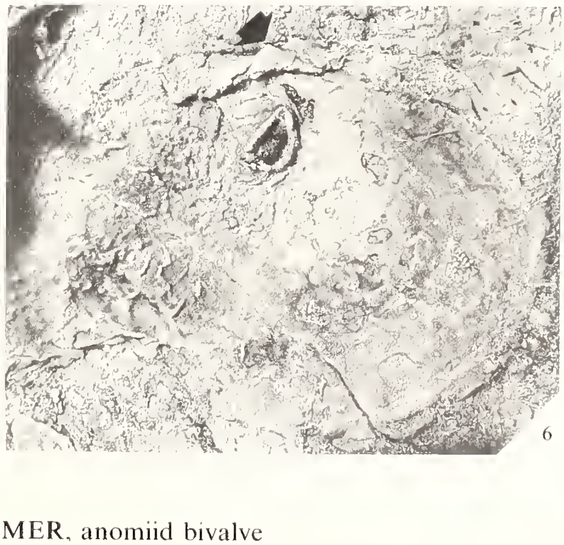
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FÜRSICH and PALMER, anomiid bivalve

as a replacement in finely equigranular calcite (either a cement or a neomorphic replacement). The circular adductor muscle scar, presumably originally of myostracal prisms, is one such structure. It occupies a subcentral position such that its ventral margin roughly occupies the geometric centre of the shell. The other formerly aragonite structure seen only in the material from this one locality is the ligamental area, from the ventral margin of which a short tooth-like process extends in a posteroventral direction. The function of this process is not clear. The ligamental area is described further below.

The most conspicuous feature of the shell is a circular hole up to 3·5 mm in diameter in the largest specimens, which occupies a position just below the hinge line and just anterior of the dorsoventral axis (Pl. 99, figs. 1–6). Close study of the growth lines of the shell around this hole clearly shows that early in ontogeny it was an open notch beneath an anterior auricle, and that it must have remained open until the animal attained a diameter of about 1 cm. After this time it became occluded by adjoining of the outer shell layers of the anterior auricle and of the anterior shell margin, which swung dorsally around the hole to cut it off. The resulting join shows up as a short groove running from the anterodorsal margin of the hole to the front end of the ligamental area (Pl. 99, fig. 2; text-fig. 1). This hole was clearly occupied by a byssus in life, and its margins are made of the foliated calcite middle shell layer. In older specimens this margin thickens and becomes raised above the level of the inside of the shell (Pl. 99, fig. 3). The byssal threads laid down early in ontogeny appear to have remained attached throughout the subsequent growth of the shell, because the dorsal margin of the hole is seen to have lifted away from the substrate (over the dorsal byssal threads), as it grew in a ventral direction. The byssal hole thus looks today like a slipper with a dorsally directed pointed toe, the point of which lies just below the umbo.

The ligament appears to have been amphidetic but the ligamental area is divided into anterior and posterior portions which are mirror images about an axis which constitutes a perpendicular dropped from the umbo. The whole ligamental area thus has the form of a dorsoventrally flattened W (Pl. 99, figs. 1–3). The ventral edge forms an increasingly steep angle with the horizontal substrate during growth, so that in adult specimens, it and the edges of the central chevron of the W appear almost vertical (in a topographic sense) in the horizontal valve. It appears that in life the ligament must have passed over the dorsal edge of this chevron, hence introducing a dorsal element into the direction of the opening thrust. From the single poorly preserved fragment of left valve, attached to one of the specimens from the Oxfordshire Oxfordian (Pl. 99, fig. 6), it appears that the central chevron fitted into a corresponding triangular notch immediately below the left valve umbo. This umbo is clearly seen to be marginal.

TAXONOMIC AFFINITIES

The distinctive byssal foramen, which originates by complete enclosure of an anterior sub-auricular notch, is clearly reminiscent of the superfamily Anomiacea. An assignation to this group is further supported by the similarity of the shell structure to that of recent anomiaceans (Taylor, Kennedy and Hall 1969; Yonge 1977). The only other Jurassic genus known to have the byssal foramen is the pulvinitid *Hypotrema*, which is characterized by a multivincular ligament and an absence of foliated calcite from the shell.

The characteristics of the extant anomiaceans have recently been extensively discussed by Yonge (1977), who distinguishes two families—the Anomiidae and the Placunidae. Yonge further characterizes Recent anomiaceans by their monomyarian, pleurothetic (on the right valve) condition; their right twisted and hypertrophied byssal apparatus; their asymmetric ligament with projecting crurum on the right valve which introduces a dorsally directed element into the direction of the ligamental opening thrust; the supradorsal extension of the mantle lobes; and the calcified byssal secretion. Of these five characteristics, the first three are clearly exhibited by our animal, the fourth is hinted at, and the last was probably absent (not being necessary in a pallially cemented animal).

The form of the ligament in our animal differs from that in any of the Recent anomiaceans, being neither the boss on the end of a crurum typical of the anomiids, nor the inverted V-shaped structure found in the Placunidae. Nevertheless, we feel that both conditions could easily have arisen from our animal by modification of the central chevron in the W-shaped ligamental area. Swelling of this area in the ventral and dorsolateral directions would produce the sort of crurum seen in the anomiid *Pododesmus* (and incidentally in the typically anomiid Cretaceous genus *Paranomia*—see Wade 1926). On the other hand, reduction of the lateral parts of the ligamental area coupled with ventral growth of the descending arms of the central chevron produces the typically placunid structure. Indeed, a similar process is seen in the ontogenic development of *Placunanomia* (Yonge 1977).

The retention of the byssal foramen into adulthood and the inferred primitive phylogenetic position of our material justifies its being placed in the Anomiidae rather than the Placunidae, but the pallial cementation, the ligament characters, the probable lack of calcification in the byssus, and the marginal umbo justify creation of a new genus.

Superfamily ANOMIACEA Rafinesque, 1815

Family ANOMIIDAE Rafinesque, 1815

EONOMIA gen. nov.

Type species. Eonomia timida sp. nov.

Derivatio nominis. eos (Greek) = dawn.

Diagnosis. Pallially cemented anomiacean with distinct byssal foramen; ligamental area shaped like a flattened W with ventral margin raised; short tooth-like process extending below umbo in a posteroventral direction; umbo in left valve marginal; byssus probably uncalcified.

Eonomia timida sp. nov.

Plate 99, figs. 1–6; text-fig. 1

Holotype. From the Upper Oxfordian (*Plicatilis* Zone), Falaises des Vaches Noires, Normandy (JZ 1782).

Paratypes. JZ 1783–1786 from same locality as holotype; JZ 1787 from hardground immediately below sponge reefs at St-Aubin-sur-Mer, Normandy (Upper Bathonian, *hollandi* subzone); JZ 1788 from hardground at top of sponge reefs on foreshore at Luc-sur-Mer, Normandy (Upper Bathonian, *hollandi* subzone); JZ 1789 from fossiliferous clay beneath Calcaire de Langrune, Lion-sur-Mer, Normandy (Upper Bathonian, *hollandi* subzone); JZ 1790 from hardground at top of Calcaire de Ranville, Ranville Cement Works, Normandy (Upper Bathonian, *aspidoides* Zone); J 40190–40199 from Upper Oxford Clay, Stanton Harcourt, Oxfordshire; J 40187–40189 from Upper Oxford Clay, Cowley (*mariae* or *cordatum* Zone); J 40184–40186 from hardground at base of Bradford Clay, Bradford-on-Avon, Wilts. (Upper Bathonian, *hollandi* subzone).

Derivatio nominis. timidus (Lat.) = shy, retiring, wary of discovery.

Diagnosis. Circular or subcircular *Eonomia* up to at least 8 cm in height; ventral edge of byssal foramen never exceeds a quarter of the distance between the umbo and the ventral margin; well-developed aragonite inner shell layer overlapped by a wide expanse of the middle foliated calcite shell layer, which forms the inner surface of the valve anteriorly, posteriorly, and ventrally.

PALAEOECOLOGY

Eonomia timida occurs in two broad habitats: under recesses and in cavities beneath hardgrounds, and on biogenic hard substrates in muddy environments. Bathonian specimens are known only from the former habitat. They occur on the walls of lithified burrow systems, on the roofs of hardground cavities or recesses, and on the lower surfaces of *Platychonia*, a lithistid sponge forming small sponge reefs at St-Aubin and Luc-ser-Mer (Normandy) (Fürsich and Palmer 1979; Palmer and Fürsich 1981). In contrast, in the Lower to Middle Oxfordian, they are known encrusting *Liostrea*, *Gryphaea*, and the vertebrae or other bones of plesiosaurs. In this case they appear to have lived on upper surfaces. The occurrence at Vaches Noires is within the oyster/*Isognomon promytiloides* association (Fürsich 1977), which occupied a low-energy, offshore environment characterized by low sedimentation rates and a fine-grained substrate. The latter was probably somewhat firmer than that represented by the bulk of the Oxford Clay.

Three possible explanations are offered for the occurrence of *E. timida* in two distinct habitats:

(*a*) The distribution pattern is a result of collection failure rather than an original feature and thus of no significance. However, in the search for further specimens of *Eonomia*, a great variety of substrates and habitats within the Jurassic have been examined, and it appears that the known distribution pattern is a primary feature.

(*b*) A shift in habitat occurred during the course of the Jurassic from cavities to exposed hard substrates, possibly in conjunction with a better adaptation to cope with water rich in suspended sediment particles.

(*c*) Bathonian and Oxfordian forms represent two different species each restricted to a particular habitat.

Although there are certain morphological differences between the two groups of specimens (e.g. a larger size of the Oxfordian specimens), we feel that they do not merit specific separation. We therefore think that a shift in habitat is the most likely explanation for the observed distribution pattern of *Eonomia*. Recent Anomiacea are particularly well adapted to life on muddy substrates as their foot serves as a highly efficient organ for cleansing the mantle cavity (Yonge 1977). It is therefore suggested that, as Bathonian forms needed clear water (usually associated with hardgrounds) and could not cope with sediment influx (hence their preference for cavity roofs) and Oxfordian forms were well adapted to live in turbid environments, the change in habitat was due primarly to the increased efficiency of the foot in cleaning the mantle cavity. The problem as to why *Eonomia* has a centrally placed byssus lasting throughout life, as well as being cemented to the hard substrate (a marked case of belt and braces) is probably also solved by a consideration of cleansing habits. Recent anomiids have a very small proportion of catch to quick muscle in the adductor, whose function is largely given over to rapid contractions of the valves to eject faeces and pseudofaeces (Yonge 1977). It is the hypertrophied byssal retractor muscle that thus takes over the business of holding the valves closed for longer periods of time.

EVOLUTIONARY SIGNIFICANCE

The early evolutionary history of the Anomiacea is very confused, and the pre-Cretaceous ranks of the superfamily are largely composed of imposters and cripples. The only serious Palaeozoic contender for a place in the group is the Permian *Permanomia* (Newell and Boyd 1970). This genus, however, like previously proposed Palaeozoic contenders (see Stoliczka 1870–71) is too poorly known to be certain of inclusion. The critical right valve is unknown (probably it too was cemented), and the anomiid designation is made on the basis of the left valve musculature and a putative calcified byssus attached to the inside of the left valve in one specimen. The unlikely position of this latter feature surely makes it more likely to be an artefact, and the left valve musculature by itself is not enough (as Newell and Boyd (1970) point out) to ensure the certain familial affinity. Similar musculature would be expected, for example, in the early Pulvinitidae. *Permanomia* further has a duplivincular ligament, although this could give rise to the simpler alivincular ligament of true anomiaceans by neotenous retention of the primary ligament (Trueman, *in* Cox 1969). The verdict on *Permanomia* therefore must be 'not proven', but even if a right valve with the appropriate shell structure and an enclosed byssal notch were found tomorrow, the difference in the ligament should surely justify a separate family within the superfamily.

References to Jurassic *Anomia* are widespread in the literature (e.g. Buvignier 1852) and we have examined material from three museums with good collections of Jurassic bivalves where examples of such *Anomia* might be expected. These collections are those of the Oxford University Museum, the British Museum (Natural History), and the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. Every single putative Jurassic *Anomia* in these collections is either totally unrecognizable, or else attributable to the genus *Placunopsis*. It is our opinion that confusion with this latter species is responsible for the vast majority, and perhaps all, of Jurassic *Anomia* records. The left valves of *Placunopsis* consisted of an inner aragonite layer and an outer foliated calcite layer which invariably became worn off in the umbonal region. Thus, when the aragonite layer was dissovled away during diagenesis, the remaining calcite layer appeared to be perforated by a hole in the umbonal region that has often been mistaken for the anomiid byssal foramen. *Eonomia timida* is therefore the earliest unequivocal anomiid known to us.

Acknowledgements. We thank the staff of the Oxford University Geological Collections and the Department of Geology and Mineralogy for technical help, and Dr. N. J. Morris for discussion, during the preparation of this paper. F.T.F. is supported by a Heisenberg Fellowship, which is gratefully acknowledged.

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A REDESCRIPTION OF THE BATHONIAN RED ALGA *SOLENOPORA JURASSICA* FROM GLOUCESTERSHIRE, WITH REMARKS ON ITS PRESERVATION

by T. L. HARLAND *and* H. S. TORRENS

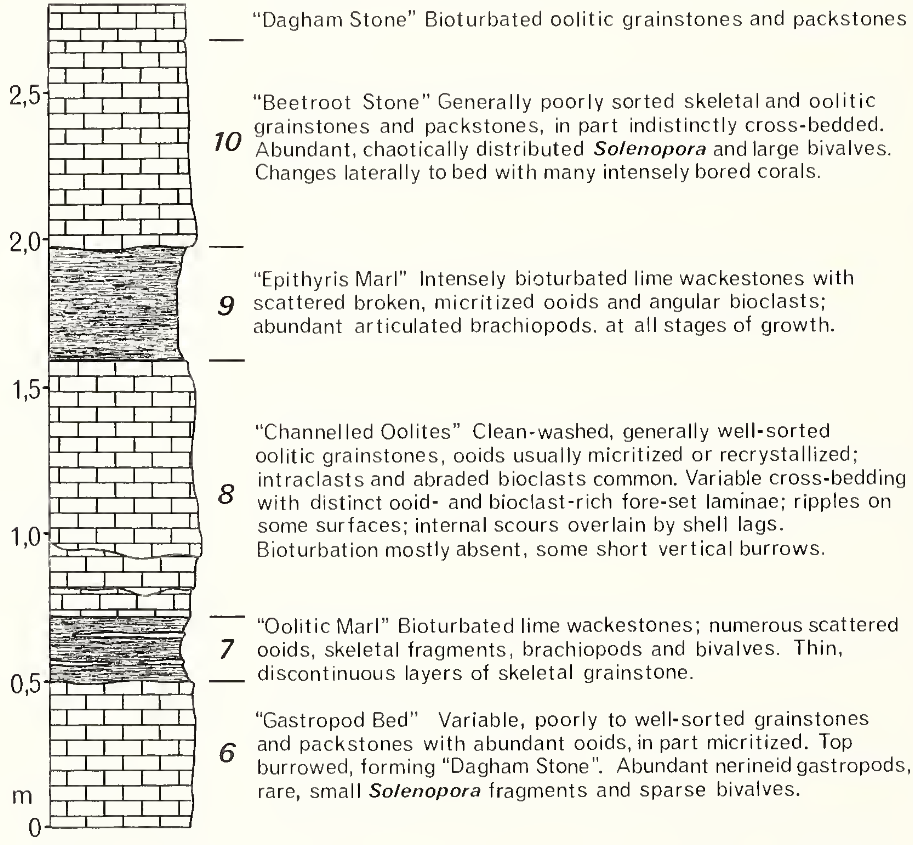
ABSTRACT. The Bathonian red alga *Solenopora jurassica* Brown 1894 ex Nicholson MSS. is redescribed and a neotype designated. It is composed of radiating filaments (0·45 mm mean diameter) divided into cells varying in length between 0·07 and 0·04 mm by concave outward septa. An alternation of layers with well-preserved and poorly preserved tissue structure respectively is typical, and parts of all specimens exhibit a bright pink banding, which is interpreted as remnants of an original pigment. Preservation of this pigment probably depended upon rapid burial of the alga while still alive or very soon after death. The only partial preservation of the pigment is related to variations of the algal tissue, which controlled later leaching.

STRIKING pink-coloured fossils from the White Limestone Formation (Bathonian) near Chedworth in Gloucestershire have been famous since they were first reported by Harker (1890, pp. 89-90) in railway sections provided by the excavation of Aldgrove cutting between Cirencester and Gloucester. Initially, these were not fully named, though they were soon identified by H. A. Nicholson as *Solenopora* Dybowski (*in* Woodward 1894, p. 290). In 1894 Brown, Nicholson's assistant, was the first to present good evidence that the specimens were fossil algae (Nicholson thought *Solenopora* to have been a 'curious extinct hydrozoan') and, using Nicholson's manuscript name, described the new species as *S. jurassica*. However, Brown differed from Nicholson in his assessment of the species. In manuscript Nicholson had seemingly only referred material from Chedworth to *S. jurassica* (see Garwood 1913, p. 469), whereas Brown extended the species to include Corallian (Upper Jurassic) material from around Malton in Yorkshire, and actually figured both a longitudinal section from Chedworth (Brown 1894, fig. 4) and a tangential section from Malton (Brown 1894, fig. 5) when erecting his species. Later, Rothpletz (1908) noted a variation in structural detail between specimens from these two horizons and areas, and proposed the genus *Solenoporella* for the Yorkshire material. This was also the opinion of Garwood (1913, p. 470), who stated, '*S. jurassica* from Chedworth represents a true species of *Solenopora* showing closely packed cells with polygonal outline in tangential section; *S. jurassica* from Malton and elsewhere in Yorkshire has distinctly circular outline in tangential section and is specifically if not generically distinct and is that described by Rothpletz as *Solenoporella*.' However, Lemoine (1928, p. 407) believed these claims to be erroneous and that *Solenoporella* Rothpletz was based on oblique rather than tangential cell cross-sections, but she unfortunately compounded the confusion by referring to Chedworth as being in Yorkshire! None of the material has been examined since this, though the material from Yorkshire, which is often silicified and poorly preserved, is presently referred to the genus *Solenoporella* Rothpletz (Dr. J. K. Wright, pers. comm. 1980). Here we redescribe *Solenopora jurassica* Brown using material only from Chedworth in Gloucestershire, resolve the problem of the unknown numbers of syntypes (now lost) from different horizons by designating a neotype, and also discuss the implications and the possible origin of the pink coloration typical of this material.

[Palaeontology, Vol. 25, Part 4, 1982, pp. 905-912, pl. 100.]

GEOLOGICAL SETTING

The large disused quarry at Foss Cross (Nat. Grid. Ref. SP 055092) near Chedworth in Gloucestershire is an extension of the former Aldgrove cutting and provides fine sections through the White Limestone Formation (Middle and Upper Bathonian). The algae under discussion here were all collected from a single bed near the top of the section at a western promontory of the quarry face, where its abundance and conspicuous pink colour led former quarrymen to term the bed 'Beetroot Stone' (text-fig. 1). Cope *et al.* (1980, p. 35, fig. 6*a*) place these beds in the Hodsoni Zone (basal Upper Bathonian) on the basis of ammonites collected both lower in this section and in the immediate district. These beds (6–11) are lateral equivalents of part of the Ardley Member further east in Oxfordshire described by Palmer (1979). Palmer (1979, p. 204) also notes that in Oxfordshire *S. jurassica* Brown is more common in the stratigraphically lower Shipton Member. The sequence at Foss Cross is dominated by cross-stratified lime sands composed primarily of ooliths and abraded skeletal material (text-fig. 1). Channelling and scouring is commonly observed and bioturbation frequently decreases downward from the tops of thick units (cf. Palmer 1979, p. 224). Deposition appears thus to have been in a predominantly moderate-to-high-energy shoaling environment where much sediment movement occurred relatively rapidly, perhaps during major storms. At other times everyday wave and current energy modified the substrate by rippling and a frequently abundant infauna colonized the higher parts of the sediment. The thin units of lime mud and shelly lime mud included in the sequence (text-fig. 1) reflect prolonged periods of low-energy deposition, probably in extensive, sheltered depressions.


"Dagham Stone" Bioturbated oolitic grainstones and packstones
2,5
"Beetroot Stone" Generally poorly sorted skeletal and oolitic grainstones and packstones, in part indistinctly cross-bedded. Abundant, chaotically distributed **Solenopora** and large bivalves. Changes laterally to bed with many intensely bored corals.
10
2,0
9
"Epithyris Marl" Intensely bioturbated lime wackestones with scattered broken, micritized ooids and angular bioclasts; abundant articulated brachiopods, at all stages of growth.
1,5
"Channelled Oolites" Clean-washed, generally well-sorted oolitic grainstones, ooids usually micritized or recrystallized; intraclasts and abraded bioclasts common. Variable cross-bedding with distinct ooid- and bioclast-rich fore-set laminae; ripples on some surfaces; internal scours overlain by shell lags. Bioturbation mostly absent, some short vertical burrows.
8
1,0
"Oolitic Marl" Bioturbated lime wackestones; numerous scattered ooids, skeletal fragments, brachiopods and bivalves. Thin, discontinuous layers of skeletal grainstone.
7
0,5
"Gastropod Bed" Variable, poorly to well-sorted grainstones and packstones with abundant ooids, in part micritized. Top burrowed, forming "Dagham Stone". Abundant nerineid gastropods, rare, small **Solenopora** fragments and sparse bivalves.
6
m
0

TEXT-FIG. 1. Relevant part of the sequence at Foss Cross Quarry showing sedimentary character and position of the 'Beetroot Stone', logged in metres. Bed numbers (6–10) follow Torrens (1969).

SYSTEMATIC DESCRIPTION

Class RHODOPHYCEAE
Subclass FLORIDEAE
Order CRYPTONEMIALES Schmitz 1892
Family SOLENOPORACEAE Pia 1927
Solenopora jurassica Brown 1894

Plate 100

Type material. Brown's species was based on an unknown number of syntypes from both Chedworth and Malton, varying in size from 'a marble to that of an orange or even larger'. As noted in the introduction, the illustrations accompanying his descriptions comprise a longitudinal section from Chedworth and a tangential section from Malton, both prepared from thin sections. According to Brown his material came from Nicholson's collections. Unfortunately the H. A. Nicholson collection held by Aberdeen University was never properly curated (Benton and Trewin 1978), and consequently the status of all the surviving specimens there is now wholly uncertain. The only surviving material of *S. jurassica* Brown which could constitute syntype material consists of two samples (Aberdeen Univ. Nos. 10676–10677) from a single hand specimen *labelled* as from Malton, Yorkshire, and three thin sections (Aberdeen Univ. Nos. 02809–02811) labelled as from Chedworth, all in a hand other than Nicholson's own (Benton 1979, p. vii). The hand specimens, which, it should be noted, are far more similar to *in situ* material from Chedworth than to that from Malton, and may thus have had labels transposed, have no cut surfaces and show no sign of having provided thin sections. Garwood (1913) also implies that specimens from Chedworth and Malton had been confused. The surviving thin sections prepared from lost Chedworth hand specimens possibly provided the basis for Brown's figure 4 (though no direct match has been made by us) but, if the labelling is correct, they cannot have contributed to Brown's figure 5, based on Malton specimens. In view of Brown's original use of material from two localities, the uncertain authenticity of all material surviving in Aberdeen, the lack of proven syntypes in any other collection examined, and the fact that *S. jurassica* Brown is the first solenoporacean to have been described from Jurassic rocks, the only satisfactory solution is to designate a neotype and provide a redescription and illustrations, and to do this in accordance with Nicholson's apparent original intention, that is, to derive the neotype from the Chedworth exposures.

Originally, the exposures at Chedworth consisted solely of the railway cutting at Aldgrove, which was measured and described by Richardson (1911, p. 107), but in the 1920s Foss Lime and Limestone Co. Ltd. extended the exposure by excavation of Foss Cross quarry, of which the earliest section was again provided by Richardson (1930, p. 270). The quarry was closed in the 1960s and the section along the western side is now protected by the Nature Conservancy as a site of special scientific interest. The material used by us was all collected from this protected section, where it is abundant in the equivalent bed (Richardson 1930, p. 270; Barker 1976, figs. 1–22) to that in the cutting which yielded Harker's and Nicholson's material and some of Brown's syntypes.

Neotype. A single polished specimen (BMNH V 60738) now deposited in the British Museum (Natural History) with four other hand specimens (BMNH V 60739–60742) which all derived from a single large alga during preparation of thin sections. Eight of these (BMNH V 60743–60750) and two other thin sections (BMNH V 60751–60752) from other specimens are also deposited in the British Museum (Natural History). The material was collected from an inverted position in the lower part of the 'Beetroot Stone' (Bed 10 of Torrens 1969) of the White Limestone Formation at Foss Cross.

Diagnosis. Solenopora exhibiting marked banding of alternating layers with well-differentiated and poorly differentiated structure; structure consisting of radiating filaments (cell columns); filaments 0·045 mm mean diameter, filament walls approximately 0·008 mm wide, and cells varying in length between 0·07 and 0·04 mm, separated by outward-concave cell walls 0·005 to 0·008 mm wide.

Description. The alga is well preserved though some areas of the growths have suffered recrystallization. A large size-range is present from rounded or ragged fragments as small as 1 cm diameter to complete though often overturned large hemispherical masses 25–30 cm basal diameter and up to 20 cm high. Occasionally the alga is seen encrusting small corals. Colour banding is characteristic, with reddish-pink, pink, or pale pink bands alternating with buff or off-white bands (Pl. 100, fig. 1). The pink coloration usually fades towards the outer parts of the masses. The alternating bands are usually of the order of 3–6 mm in width but occasionally much finer

(Pl. 100, figs. 1, 2). Numerous variably sized borings are present in the growths, the larger examples infrequently containing *in situ Gastrochaena* sp. or '*Lithophaga*' sp. bivalves, and the surfaces of the algal colonies are often encrusted by oysters, bryozoans, and serpulids. Distortion of algal cell structure is seen in several areas beneath encrusting organisms but this is not always the case. In addition to the epifauna the colonies usually have a crusting of coarse skeletal sediment and clean natural surfaces are rarely encountered. Many of the features described below from thin sections, including the characteristic radiating filaments, can also be distinguished in broken or worn hand specimens.

In thin section the closely packed filaments (cell columns) are seen to radiate from the lower areas upwards and outwards to the exterior; the filaments are generally straight or slightly curved (Pl. 100, figs. 4, 6) but exceptions are common, particularly near the bases of growths and around sediment incursions where the structure may be chaotic and the filaments contorted. Cross-sections show the filaments to be most commonly adpressed, forming regular hexagonal to irregularly polygonal patterns (Pl. 100, figs. 5, 7) but they may also be loosely packed, in which case they have approximately circular cross-sections; all patterns can be and usually are present within the larger growths. The cells are mostly filled with calcite spar and differentiation between them and dark wall material is simple. Where micritic sediment infills the cells some difficulty is experienced in delimiting this from wall material. Mean diameter of filaments mid-wall to mid-wall, 0·045 mm (observed range 0·029 to 0·059 mm); mean cell diameter 0·039 mm (observed range 0·024 to 0·056). Thickness of wall material is from 0·001 to 0·02 mm, although these are rare extremes (the former noted in a specimen shown by deformed sediment-filled borings to have undergone post-mortem crushing and the latter in the lower, chaotic parts of one specimen); mean thickness of wall material 0·008 mm (usual range 0·005 to 0·01 mm), and shows slight irregularities along its length. The walls nowhere exhibit any internal structure.

In vertical section the characteristic banding is clearly seen to arise from the alternation of layers with well-defined structure dominated by filament walls (Pl. 100, figs. 4, 6, 8) and layers with poorly defined structure where filament walls are inconsistent (Pl. 100, figs. 3, 6). Pink colour most commonly corresponds with layers of poorly defined structure. Mostly, the filaments run adjacent and are approximately parallel to each other; bifurcation is quite frequent but is inconspicuous, occurring randomly and sparsely throughout the body of the growths. The medium-sized and larger masses usually include elongate sediment-filled 'cracks' several centimetres long, up to 0·5 cm wide and oriented perpendicular to the banding (Pl. 100, fig. 1). Adjacent filaments curve gently towards these 'cracks', which are not borings but features of the original growth form. Banding is seen deflected downwards towards these features, indicating that the upper surface during growth was mammillated. The filaments are divided into cells by frequent cell walls which are gently outward-concave (Pl. 100, fig. 8). Cell walls are composed of the same material as filament walls but are generally slightly thinner, ranging from 0·004 to 0·01 mm. The cell walls divide the filaments into discrete cells 0·07 to 0·04 mm (most usually 0·07 to 0·25 mm) long. In layers where the stucture is well defined, cell walls in adjacent filaments are

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EXPLANATION OF PLATE 100

Polished slab and photomicrographs of *Solenopora jurassica* Brown from the 'Beetroot Stone' at Foss Cross quarry, Chedworth. All specimens in the British Museum (Natural History), London.

Fig. 1. Slab showing polished surface of neotype, which shows the typical colour banding and 'cracks' widening into more deeply coloured bands. Also note sediment incursions (arrowed). Numbered scale in cm. BMNH slide V 60738.

Fig. 2. Longitudinal section from neotype, showing tissue banding. × 14. BMNH slide V 60743.

Fig. 3. Longitudinal section, showing grid-like nature of tissue layers with poorly preserved filaments. × 55. BMNH slide V 60752.

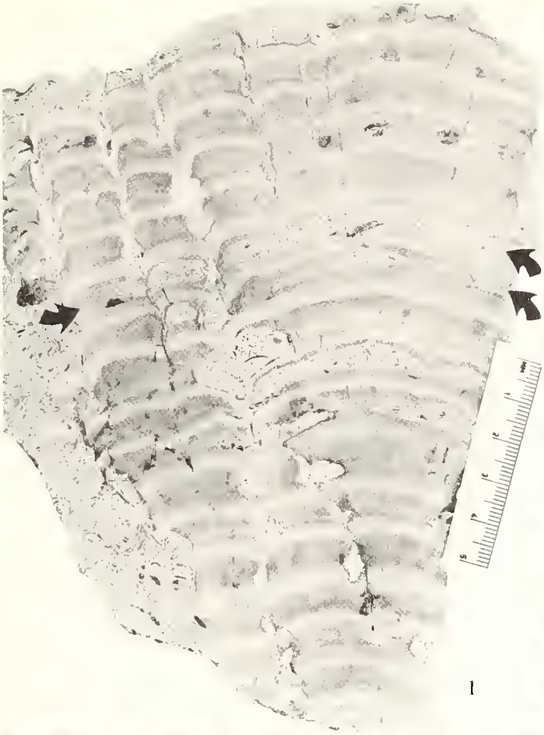
Fig. 4. Longitudinal section, showing nature of tissue layers with well-preserved filaments. × 50. BMNH slide V 60751.

Fig. 5. Transverse section from neotype, showing regular polygonal cell cross-section. × 35. BMNH slide V 60744.

Fig. 6. Longitudinal section from neotype, showing well-preserved filaments changing upwards into layer with less well preserved filaments. × 25. BMNH slide V 60743.

Fig. 7. Transverse section, showing close-up of spar-filled cells. × 120. BMNH slide V 60747.

Fig. 8. Longitudinal section, showing upward-concave divisions dividing filaments into cells. × 150. BMNH slide V 60749.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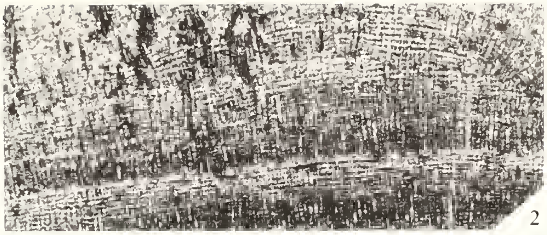
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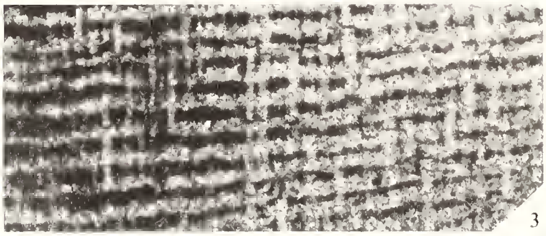
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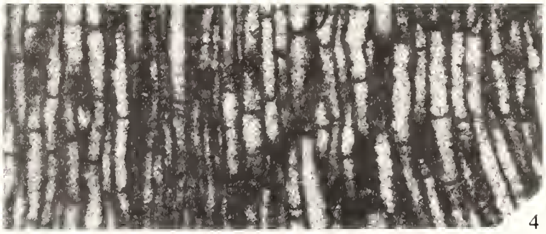
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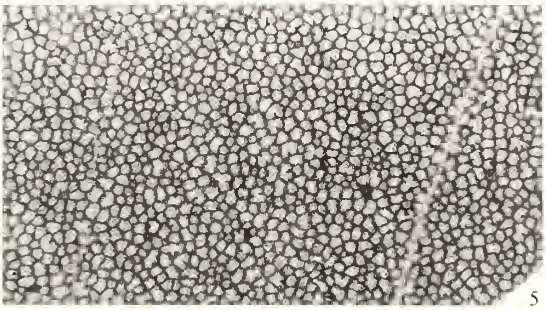
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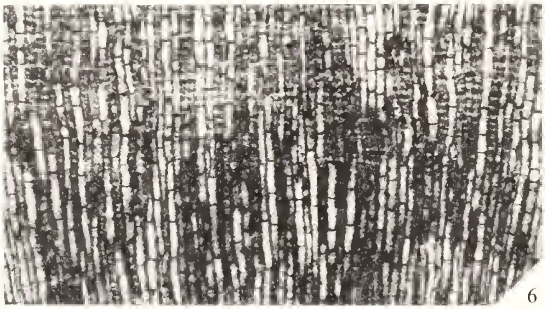
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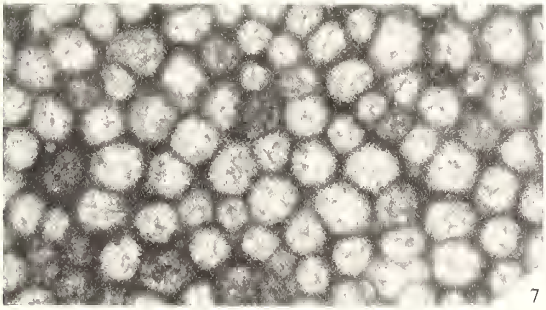
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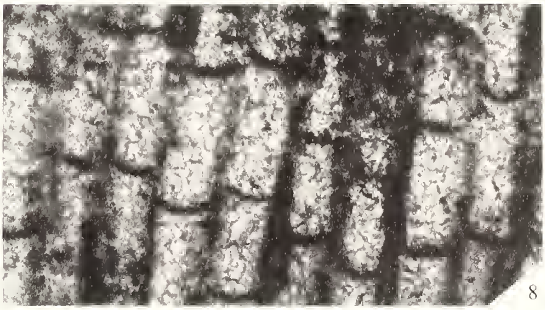
8

HARLAND and TORRENS, *Solenopora jurassica* typically randomly placed but occasionally they occur at the same level across several filaments. This contrasts with layers of poorly defined structure, where the septa are often more prominent than tubule walls and frequently occur at the same level across numerous tubules. This results in a grid-like or even concentric appearance. The concentric appearance is also often accentuated by recrystallization along thin layers (0·035 to 0·04 mm thick) which alternate with preserved tissue (Pl. 100, fig. 3). Rare, well-defined filaments or groups of two-to-five filaments pass through these bands and similar groups originate close to the top of the bands and continue upwards into suprajacent bands with well-preserved structure throughout. Smooth irregularities in the banding, in the form of crescentic outgrowths from the top of the bands of poorly defined structure, are common and supplement the mammillated growing surface noted above.

Neither hypothallic tissue (basal layers of unusually large cells) nor reproductive features (sporangia, conceptacles) have been noted.

REMARKS

A number of authors have commented on the presence of a strong pink colour in specimens of *S. jurassica* Brown (e.g. Garwood 1913; Lemoine 1928; Cailleteau 1966) and banding of tissue is known in species of *Solenopora* from the Ordovician until extinction in the late Jurassic (Johnson 1960, 1961, 1963, 1964). Lemoine (1928, p. 406) suggested that the pink colour was an original feature, preserved by rapid burial of live algae. Work in progress by the authors and others has so far confirmed the presence of organic pigments and suggests that they are probably porphyrins. Further analyses are being performed in an attempt to ascertain the exact compounds involved.

Sediments comprising the White Limestone Formation to the east of Chedworth were deposited in a complex mosaic of shallow subtidal and occasionally intertidal or supratidal environments developed on or near the London Platform, between the north-easterly London Land Mass and the offshore, deeper-water south-westerly Severn Basin (Palmer 1979). Beds composed of abundant *in-situ* or storm-disrupted coral colonies are common throughout the White Limestone in that area, and Palmer (1979, p. 213) likens those found in Oxfordshire to modern *Porites* shoals and thickets present in shallow water (about 3 m depth) in the Florida Keys. He also notes the lack of algae in the Oxfordshire coral beds when compared to their modern equivalents, where *Goniolithon* (Rhodophyceae) and *Halimeda* (Chlorophyceae) are common, and suggests this exclusion results from high water-turbidity caused by suspended fines from the nearby London Land Mass. However, reports of algae in the White Limestone further west are much more common (e.g. Richardson 1930, 1933; Torrens 1967; Elliott 1975). As noted above, the sedimentary character of the sequence in which *S. jurassica* Brown occurs at Foss Cross (text-fig. 1) and of the White Limestone as a whole in the area around Chedworth is indicative of variable high-to-moderate-, occasionally low-, energy conditions and an environment of intermittently shifting variable skeletal substrates, which were often oolite-rich, cut by storm-generated and storm-maintained channels or scours (cf. Klein 1965; Fürsich and Palmer 1975; Silva 1976). This indicates that the Chedworth area was sited at the edge of the London Platform shelf, where higher energy levels and greater water exchange resulted in reduced turbidity and permitted a more profuse flora and the local development of algal shoals. Ware and Windle (1981) describe a similar, slightly shallower situation for the overlying Forest Marble Formation near by. Within this sedimentary framework it is easy to envisage storm or tidal current disruption of benthic organisms and their rapid burial in channels or beneath migrating shoals, and we interpret the 'Beetroot Stone' at Foss Cross as one such storm-disrupted and rapidly buried algal shoal. The *Solenopora* themselves also suggest disruption and rapid burial. Direction of growth is shown clearly by the banding, and counts indicate that at least 62% of studied specimens (*c.* 50) were preserved in an orientation other than that of life. Borings and particularly epifauna are, however, concentrated on the upper parts (life orientation) of the algal masses. Large bivalve and other irregular borings were only noted into the upper growth surfaces of specimens and many of the smaller, thin tubular borings (?*Trypanites*) are seen to originate within the masses at marked growth lines, indicative of overgrowth by tissue, that is, formation during growth. Encrusting oysters and serpulids have again only been noted on the same tops or upper sides of specimens and, although several have been noted spreading along the sides and basal parts of masses, the majority of bryozoan encrustations are also concentrated at the tops of masses. This evidence, together with their very large size range and chaotic sorting, supports the idea of disruption and a rapid and total burial, killing the alga, preserving the original pigment and preventing further colonization by boring or encrusting organisms.

The alternating bands of colour closely correspond with variations in the structure of the algae, the pink bands relating to layers of tissue with poorly defined structure. It seems possible that the colour banding originated during the life of the alga and Lemoine (1911) has suggested that colouring matter is produced in living algae more abundantly at some times than others, though not necessarily relating to distinct growth phases. However, several features observed in the Chedworth specimens argue against this. First, although the pinkish coloration relates most commonly to the bands of poorly defined tissue, this is not always the case. Secondly, even within these bands there is usually a fading of the colour towards the perimeters of the masses. This strongly indicates that the whole of the algal masses were originally coloured and that subsequent leaching has taken place around the edges of the buried masses. Leaching has also taken place along the sides of the 'cracks' noted in the earlier description, as again the colour fades towards these features. The distribution of preserved pigment can thus be best explained as follows: leaching preferentially removed original pigment from the perimeters of the masses and along sediment-filled 'cracks' or borings and also from layers of tissue with well-defined radial structure which were more porous. The more compact, concentric arrangement within the layers of tissue with poorly defined structure coupled with preferential recrystallization significantly reduced porosity in these layers and served to decelerate or prevent leaching. The origin of the differentiation of the algal tissue into these alternating bands is unknown but it is tempting to propose a seasonal influence. Whatever the cause, this alternation of tissue appears to be the prime factor in the preservation of the original pigmentation after burial of the alga.

Acknowledgements. We gratefully acknowledge help from Drs. G. F. Elliott, P. D. Lane, and T. J. Palmer, who each suggested improvements to our original manuscript. Joan Cliff typed the final manuscript and David Kelsall produced photographs for the plate.

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THE PALAEONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1981

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,498 on 31 December 1981, a decrease of 35 over the previous year. There were 956 Ordinary Members, an increase of 6; 28 Retired Members, an increase of 13; 159 Student Members, a decrease of 32; and 355 Institutional Members, a decrease of 1. The number of institutions subscribing to *Palaeontology* through Marston's agency was 419. Subscriptions to *Special Papers in Palaeontology* numbered 164 individual (the same total as for 1980) and 138 Institutional, an increase of 3 since 31 December 1980. Subscriptions to *Special Papers* through Marston's agency fell sharply to approximately 79, a decrease of 41. Sales of back parts of *Palaeontology* via the Membership Treasurer totalled 5 transactions, realizing £19, a very sharp drop from £180 in 1980. Sales of back copies of *Special Papers* fell to 64 transactions, realizing £893. Sales of back parts of *Palaeontology* to Institutional Members yielded £150 plus U.S. $505. Sales of *Special Papers* to Institutional Members yielded £242 plus U.S. $301.

FINANCE. During 1981 the Association published Volume 24 of *Palaeontology* at an estimated cost of £47,186 (including £5,746 postage and distribution). *Special Papers 26* and *27* were published at a cost of £9,217. The Association is grateful to all who made donations; a generous donation from Mrs. Sylvester-Bradley has enabled the Association to establish a fund granting annual research awards.

PUBLICATIONS. Volume 24 of *Palaeontology*, published in four parts during 1981, contained 36 papers totalling 890 pages and 126 plates. *Special Paper 26*: 'The fine structure of graptolite periderm' was published in January 1981 and *Special Paper 27*: 'Late Devonian acritarchs from the Carnarvon Basin, Western Australia' in February 1981.

MEETINGS. Nine meetings were held during 1981. The Association is indebted to the organizers, hosts, and field leaders.

a. *A Field Meeting* on 'Tertiary carbonate facies and faunas of Malta' was held on 2–9 January and led by Dr. D. W. J. Bosence, Dr. H. M. Pedley, and Dr. E. P. F. Rose. Twenty-seven attended. The local Secretary was Dr. E. P. F. Rose.

b. *A Working Group* on 'Facies and faunas of the Tethyan Tertiary' was held on 4 February at Bedford College, London. Thirty attended the meeting. The local Secretary was Dr. E. P. F. Rose.

c. *A Review Seminar* on 'Brachiopod palaeoecology' was held on 18 February at the British Museum (Natural History). Ninety-four attended the meeting. The local Secretary was Dr. L. R. M. Cocks.

d. *The Twenty-fourth Annual General Meeting* was held in the Lecture Theatre of the Geological Society of London on 18 March. Dr. P. M. Kier (U.S. National Museum) delivered the Annual Address on 'Rapid evolution in echinoids'.

e. *A Field Meeting*, organized by the Carboniferous Group, to the 'Carboniferous of north-west Germany' was led by Dr. W. Kasig and Dr. E. Paproth. Forty-six attended the excursion, which was held on 23–28 April.

f. *A Review Seminar* on 'Reconstructing Coal Measures' vegetation' was held on 6 May at the University of Manchester. Seventy attended the meeting. The local Secretary was Dr. J. Watson.

g. *A Field Meeting* on 'Eocene and Oligocene of the Isle of Wight' was held on 25–28 September and led by Dr A. N. Insole. Five attended.

h. *A Review Seminar* on 'Precambrian–Cambrian evolutionary explosion' was held on 11 November at the University of Bristol. One hundred and thirty attended. The local Secretary was Dr. J. W. Cowie.

i. *The Annual Conference*, held at the University of Exeter on 17–20 December, combined an open meeting with the theme 'Palaeontological criteria for the recognition of deeper water sediments'. One hundred and thirty-five attended. The President's Award was made to Miss J. Francis. An excursion led by Dr. E. B. Selwood, Mr. P. Turner, and Mr. M. Whitely visited the Devonian and Carboniferous rocks of the Launceston area. The local Secretary was Professor J. W. Murray.

COUNCIL. The following members served on Council following the A.G.M. on 18 March 1981: *President*, Dr. W. H. C. Ramsbottom; *Vice-Presidents*: Professor C. B. Cox, Professor J. W. Murray; *Treasurer*: Mr. R. P. Tripp; *Membership Treasurer*: Dr. J. C. W. Cope; *Secretary*: Dr. R. Riding; *Marketing Manager*: Dr. R. J. Aldridge; *Editors*: Dr. K. C. Allen, Dr. M. G. Bassett, Dr. L. R. M. Cocks, Dr. R. A. Fortey, Dr. A. L. Panchen; *Other Members*: Dr. D. E. G. Briggs (Circular Reporter), Dr. C. H. C. Brunton (Institutional Membership Treasurer), Dr. R. Harland, Dr. A. R. Lord, Dr. J. Miller, Dr. T. J. Palmer, Dr. M. Romano, Dr. D. J. Siveter, Dr. P. W. Skelton, Dr. P. D. Taylor, Dr. A. T. Thomas, Dr. H. S. Torrens, Dr. N. H. Trewin, Dr. J. Watson.

CIRCULARS. Four Circulars, numbers 103–106, were distributed to Ordinary, Retired, and Student Members, and on request to over 100 Institutional Members during 1981.

COUNCIL ACTIVITIES. During 1981 overseas field meetings were organized in Malta and West Germany. The Malta Field Guide was published in a similar format to the Devonian Symposium (PADS) guides in 1978. The one-day Review Seminars introduced in 1980 were continued and attracted large audiences.

With generous support from Mrs Sylvester-Bradley Council was able to establish a fund in memory of Professor Peter Sylvester-Bradley to encourage palaeontological research. The first awards from the fund are expected in 1982.

Future meetings will follow the now established programme of conferences, field meetings, and seminars. Council plans to introduce a new booklet series, to sponsor other palaeontological publications, and to introduce review articles in *Palaeontology*.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1981

BALANCE SHEET AS AT 31 DECEMBER 1981

1980 £	1980 £		£	£
		CURRENT ASSETS		
	35,891	Investments at cost (see schedule)	45,843	
	–	Burgess Shale Portfolio	500	
	1,873	Sundry debtors	2,135	
	16,957	Cash at bank	12,880	
54,721				61,358
		CURRENT LIABILITIES		
	1,702	Subscriptions received in advance	881	
	11,500	Provision for cost of publication of *Palaeontology*	12,000	
	–	Sylvester Bradley Fund	2,010	
	767	Sundry creditors	1,959	
	1,625	Provision for Meeting Reserve	2,290	
15,594				19,140
£39,127				£42,218

Represented by:

PUBLICATIONS RESERVE ACCOUNT

1980 £	1980 £		£	£
	24,584	Balance brought forward	39,127	
	14,543	Excess of income over expenditure for the year transferred from Income and Expenditure Account	3,091	
£39,127				£42,218

Income and Expenditure Account for the Year Ended 31 December 1981

INCOME

1980 £		£	£
	Subscriptions for 1981	34,108	
	Subscriptions for 1980	141	
27,885			34,249
	Palaeontology—Sales	22,712	
	—Donations	408	
14,918			23,120
	Special Papers— Sales	4,068	
	Donations	467	
19,987			4,535
—	Receipt from Carnegie Trust		500
1,322	Offprints profit/(loss)		(18)
816	Profits less losses on sales of investments		—
6,479	Investment Income (see Schedule)		6,582
£71,407			£68,968

EXPENDITURE

1980 £		£	£
	Cost of publication of *Palaeontology*:		
	Volume 24, Part 1	12,061	
	Part 2	11,262	
	Part 3	11,863	
	Part 4	12,000	
	Under provision for Volume 23 Part 4	799	
43,806			47,985
	Cost of publication of *Special Papers*:		
	No. *26*	5,649	
	No. *27*	3,568	
7,137			9,217
	Cost of Circulars:		
	Preparation	4,211	
	Postage	1,031	
	Credit	(579)	
3,247			4,663
	Administrative expenses:		
	Postage and stationery	1,020	
	Editorial expenses	214	
	Sales Promotion	264	
	Meeting expenses	1,705	
	Membership of Societies	50	
	Audit fee	259	
	Grant and awards	500	
2,674			4,012
£56,864			£65,877
£14,543	Excess of income over expenditure for the year transferred to Publications Reserve Account		£3,091

SCHEDULE OF INVESTMENTS AND INVESTMENT INCOME AS AT 31 DECEMBER 1981

		Cost £	Gross Income for Year £
£12,000	13¼% Exchequer Stock 1987	11,520	1,590
£1,000	9% Treasury Stock 1992/1996	991	90
£1,000	9% Treasury Stock 1994	955	90
£4,000	8% Treasury Stock 2002/2006	2,192	320
£5,357	13¼% Treasury Stock 1997	5,000	710
£3,280	13¼% Exchequer Stock 1996	3,000	435
£2,000	Agricultural Mortgage Corporation Ltd. 9¼% Debenture 1980/1985	1,938	185
5,270	M. & G. Charifund units	4,073	938
£2,000	Imperial Group Ltd. 8% Convertible Unsecured Loan Stock 1985/1990	1,405	160
10,000	New Throgmorton Trust Ltd. 25p Income Shares	1,706	414
1,600	Commercial Union Assurance Co. Ltd. 25p Shares	2,157	257
5,000	Thorn EMI Ltd. 7% Convertible Redeemable Second Cumulative Preference £1 Shares 1992/1999	5,009	250
1,000	Clarke, Nicholls & Coombs Ltd. 25p Shares	954	57
6,180	M.E.P.C. Ltd. 6½% Convertible Unsecured Loan Stock 1995/2000	4,943	402
			5,898
	Bank interest (net)		684
		£45,843	£6,582
	Market value at 31 December 1981 (1980—£41,242)	£48,977	

Report of the Auditors to the Members of The Palaeontological Association. In our opinion the accounts as set out on pages 2 to 4 give a true and fair view of the state of the affairs of the Association at 31 December 1981 and of its income and expenditure for the year ended on that date.

D. J. CAREY & CO.
Chartered Accountants

Chislehurst, Kent, January 1982

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A

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A CUMULATIVE
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M. G. BASSETT *and* V. K. DEISLER

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INTRODUCTION

In 1982 The Palaeontological Association celebrated its twenty-fifth anniversary. To mark this event in its publication programme, the Council agreed that it would be appropriate to produce a cumulative index to volumes 13 to 25 of the Association's journal, *Palaeontology*, as an accompaniment to the index to volumes 1 to 12 that was published in 1971. Each of the annual volumes itself contains a brief index as an immediate guide to the contents, but the aim of this cumulative index is to give a somewhat wider coverage, cross-referenced in a number of ways as noted below. Most subjects included in the journal lend themselves readily to retrieval under three headings, namely *Systematic and General*, *Stratigraphical*, and *Geographical*, and in addition we have provided a full list of authors and titles of all papers published in the relevant volumes together with dates of publication of each part.

Author List

The 611 papers published in volumes 13-25 of *Palaeontology* are listed in alphabetical order of authorship, with two or more papers by the same author(s) in chronological order of publication. Multiple authorships are inserted in sequence under the first author's surname, and cross-references are then given for second and subsequent authors. The year of publication, title, volume number (**bold type**), part number (in parentheses), page numbers, and plate numbers are given in full for each paper. The reference number (*italic type*) at the beginning of each entry is quoted in all cross-references to that paper in the systematic and general, stratigraphical, and geographical indexes.

Systematic and General Index

Entries in this index are listed under major systematic divisions of fossils and other general subject headings, arranged in alphabetical order. The systematic breakdown adopted is mainly at the Phylum or Class level, with any other categories reflecting a practical convenience in referring to commonly studied fossil groups. Notable exceptions are the fishes, which are all listed under Pisces, and all macroplants which are listed simply within Plantae or Algae. Apart from constraints of space, we have considered it unnecessary to list all the genera and species described in the volumes since these are included in the annual indexes, which should thus be used in conjunction with the present compilation. Over and above any taxonomic subjects, many papers also include some discussion of more general topics such as evolutionary relationships, palaeoecology, biogeography, stratigraphy etc.; these general subjects are not indexed separately unless they form a major component of a paper, usually mentioned as a theme in the title or abstract. The overall scope of a paper can be checked initially by cross-reference to the title in the author list.

Entries under each heading are broken down further either under a general subheading, or more usually wherever possible are arranged stratigraphically by geological System, listed from oldest to youngest. Subdivisions of Systems (usually at Series level) are used within each entry where appropriate, and the geographical scope of a topic is given by reference to a country. Papers covering more than one System or country are indexed under each separate heading; in a few cases it has been more appropriate to use a subheading at Erathem level, and these entries are listed before those of the included Systems. If no stratigraphical and/or geographical details are given, it can be assumed that the scope of a topic covers a broader chronological or regional range. Within each subheading the entries are listed in order of publication. The volume number (**bold type**), first page number of the paper in which the topic appears, and the reference number (*italic type* in parentheses) of the paper as identified here in the author list are given for each entry.

Stratigraphical Index

All the entries in this index are cross-referenced directly from the Systematic and General Index, arranged in order of age under the chronostratigraphical headings noted above. In using stratigraphical terminology throughout these indexes, no account is taken of inconsistencies from paper to paper (e.g. upper, lower, early, late—capitalized or otherwise), but the usage adopted by authors is generally quoted if the meaning is clear. Ideally it would have been useful to include a breakdown into finer stratigraphical units, particularly by reference to well known horizons such as the Burgess Shale, Inferior Oolite, London Clay etc., but such detail is impossible in the space available, and the users of this index should be familiar with the relationships of finer classifications to the levels adopted here.

Geographical Index

The countries included in entries in the Systematic and General Index are arranged in alphabetical order. Further breakdown is then under subheadings of systematic fossil groups, with each entry giving information on broad geological age and additional details of geographical location, mostly by state, county, or major region within a country. As with the other indexes, limitations of space preclude more detailed reference to specific localities, but the coverage here gives a background guide to the regional scope of papers in the journal.

Dates of Publication

The publication dates given for the individual parts of volumes are the dates of distribution as provided by the printer (Oxford University Press). Where relevant in questions of taxonomic priority, these dates can be taken as definitive.

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AUTHOR LIST

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SILURIAN (*cont.*):

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ORDOVICIAN

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Carpoidea

ORDOVICIAN

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SILURIAN
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D

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EOCENE
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SILURIAN
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JURASSIC
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TERTIARY
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BRYOZOA
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CRINOIDEA
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ECHINOIDEA
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FORAMINIFERA
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MAMMALIA
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F

Foraminifera

GENERAL
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PERMIAN
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JURASSIC
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CREATCEOUS
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PALAEOCENE
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EOCENE
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OLIGOCENE
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NEOGENE
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MIOCENE
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AMMONOIDEA

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BRACHIOPODA

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BRYOZOA

Middle Jurassic *Terebellaria*, England and France, **21,** 357 (*540*).

CEPHALOPODA

Flow patterns and drag coefficients of shells, **19,** 539 (*101*). Role of body extension in locomotion, **23,** 445 (*102*).

CONODONTOPHORIDA

Apparatus as food-gathering mechanism, **17,** 729 (*339*).

CRINOIDEA

Silurian *Promelocrinus*, England, **19,** 651 (*82*).

CYSTOIDEA

Exothecal pore-structures, **15,** 1 (*421*). Ordovician Hemicosmitidae, Norway, Sweden, U.S.S.R., **22,** 363 (*61*).

ECHINODERMATA

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ECHINOIDEA

Coronal pores, **21,** 759 (*504*). Tube feet and ambulacral pores in irregular forms, **23,** 39 (*505*). Palaeobiology of irregular Senonian forms, England, **25,** 11 (*216*).

MAMMALIA

Carnivorous forms, **20,** 237 (*485*).

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TRILOBITA

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EOCENE

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OLIGOCENE

Trichothyriaceous fungi, England, **23,** 205 (*509*).

G

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GENERAL

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CAMBRIAN

New fauna, Antarctica, **19,** 247 (*501*).

ORDOVICIAN

Tremanotiform Bellerophontacea, U.S.A., **15,** 412 (*424*). New Ashgill pleurotomariacean, Scotland, **18,** 385 (*425*).

SILURIAN

Tremanotiform Bellerophontacea, U.S.A., **15,** 412 (*424*). New Llandovery–Wenlock pleurotomariacean, Scotland, Canada, U.S.A., **18,** 385 (*425*). Palaeoecology of Llandovery–Přídolí faunas, Canada, **21,** 285 (*426*).

JURASSIC

Symbiosis with Bathonian ectoprocts and crabs, France, **16,** 563 (*412*).

CRETACEOUS

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EOCENE

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PLEISTOCENE

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ORDOVICIAN

Tristichograptus, Spitsbergen, **14,** 188 (*202*). Development of *Glyptograptus*, Canada, **14,** 478 (*274*). Arenig–Llanvirn *Isograptus*, Australia and New Zealand, **16,** 45 (*132*). Branching in new Tremadoc *Clonograptus*, Canada, **16,** 707 (*275*). Caradoc–Ashgill faunas, eastern U.S.A. and

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SILURIAN

Fauna of Grieston Quarry, Scotland, **13,** 511 (*558*). Ludlow–Přídolí monograptids, Canada, **15,** 579 (*277*).

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Lochkovian–Pragian monograptids, Canada, **15,** 579 (*277*)

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CAMBRIAN

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CARBONIFEROUS

Westphalian palaeodictyopteran nymphs, England, **15,** 662 (*598*).

PERMIAN

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M

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CAMBRIAN

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JURASSIC

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Mammalia

GENERAL

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JURASSIC

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EOCENE

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OLIGOCENE

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CARBONIFEROUS

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ORDOVICIAN

Upper Ordovician chitinozoan fauna, U.S.A., **13,** 261 (*289*). Tremadoc acritarchs *Priscogalea* and *Cymatiogalea*, England, **17,** 41 (*446*). Reworked acritarchs in type Caradoc Series, England, **25,** 119 (*566*).

SILURIAN

Wenlock acritarchs, Canada, **16,** 799 (*557*). New excystment mechanism in Llandovery acritarch *Diexallophasis*, U.S.A., **21,** 869 (*449*).

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JURASSIC
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Distribution of dinoflagellate *Wetzeliella*, England, Belgium, Germany, **19,** 591 (*137*). Dinoflagellate cysts, England, **23,** 475 (*338*).

OLIGOCENE
Distribution of dinoflagellate *Wetzeliella*, England, Belgium, Germany, **19,** 591 (*137*). Dinoflagellate cysts, England, **23,** 475 (*338*).

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Dinoflagellate cyst *Protoperidinium*, **25,** 369 (*242*).

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Role of body extension in locomotion, **23,** 445 (*102*).

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CARBONIFEROUS
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New Asselian podocopid and its muscle-scar field, U.S.S.R., **18,** 551 (*229*).

JURASSIC
Lower Lias fauna, England, **14,** 642 (*346*). New Liassic genera *Wicherella* and *Gramannella*, England, **15,** 187 (*347*). Domerian-Toarcian faunas, England, **17,** 599 (*348*). Freshwater fauna, India, **18,** 207 (*226*). Portlandian (Purbeck) freshwater fauna, England, **18,** 419 (*37*).

CRETACEOUS
New taxa with phosphatized appendages, Brazil, **15,** 379A (*45*). Maastrichtian *Hornibrookella*, Saudi Arabia, **20,** 483 (*7*).

PALAEOCENE
Hornibrookella, Saudi Arabia, **20,** 483 (*7*). New trachyleberid genus, Saudi Arabia and Pakistan, **24,** 877 (*502*).

EOCENE
Assemblages and depositional environments, England, **20,** 405 (*301*). New trachyleberid genus Pakistan and India, **24,** 877 (*502*).

OLIGOCENE
Sannoisian faunas, north-west Europe, **15,** 267 (*300*).

PLIOCENE
New faunas, Colombia and Peru, **23,** 97 (*499*).

QUATERNARY
New limnocytherid genus, Argentina, **17,** 669 (*591*).

PLEISTOCENE
New sub-Recent *Hemicypris*, Kenya, **13,** 289 (*43*). *Hemicypris*, Kenya, **15,** 184 (*44*). Beestonian-Cromerian freshwater assemblages, England, **22,** 293 (*154*). New faunas, Colombia and Peru, **23,** 97 (*499*).

RECENT
Hemicypris, Kenya, **15,** 184 (*44*).

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P

Palaeocommunities

See Palaeoecology.

Palaeoecology

GENERAL

Vertebrate faunal replacement on Permo-Triassic continents, **14,** 131 (*464*). Ecological succession in intraformational hardgrounds, **17,** 949 (*221*). Interrelationships of early terrestrial arthropods and plants, **18,** 391 (*320*). History of seagrass communities, **18,** 681 (*70*). Floating orientations of cephalopod shell models, **23,** 931 (*450*).

ALGAE

Habitats of transported Middle Jurassic microflora, England, **18,** 351 (*179*). Free-living coralline forms, Ireland, **19,** 365 (*62*).

AMMONOIDEA

Middle Cretaceous *Scaphites* facies, Japan, **22,** 609 (*529*).

ANTHOZOA

Sedimentological factors affecting distribution and growth, Carboniferous, Ireland, **13,** 191 (*263*). Pleistocene reef succession and diversity, Kenya, **23,** 1 (*141*). Ecological stratification in Pleistocene reefs, Kenya, **24,** 609 (*142*).

AVES

Upper Eocene penguin, Australia, **17,** 291 (*286*).

BELEMNOIDEA

Upper Cretaceous faunas, England and France, **23,** 889 (*282*).

BIVALVIA

Periodicity structures and growth controls in Recent *Cerastoderma*, England, **14,** 571 (*189*). Periodicity structures and stunting in Recent *Cerastoderma*, Wales, **15,** 61 (*190*). Trophic group and evolution, **17,** 579 (*337*). Miocene-Recent Glycymerididae, **18,** 217 (*551*). Burrowing and coadaptation in Mesozoic-Cenozoic Trigoniidae, **20,** 869 (*517*). Physiological differences from brachiopods in determining community evolution, **22,** 101 (*519*). Jurassic *Hiatella*, England, **23,** 769 (*302*).

BRACHIOPODA

Late Silurian-early Devonian gypidulids, U.S.A., **16,** 381 (*16*). Epizoan encrustation on Silurian faunas, Sweden, **17,** 423 (*269*). Environmental factors determining distributions, **17,** 879 (*212*). Devonian *Uncinulus*, Spain, **18,** 367 (*588*). Food and feeding processes, **19,** 417 (*518*). Physiological differences from bivalves in determining community evolution, **22,** 101 (*519*). Anomalous occurrences of Ordovician-Silurian *Schizocrania*, England and Wales, **23,** 707 (*340*). Ecology and population structure of Recent *Terebratulina*, Scotland, **25,** 227 (*146*).

BRYOZOA

Symbiosis between Jurassic ectoprocts, gastropods and crabs, France, **16,** 563 (*412*).

CRUSTACEA

Symbiosis between ectoprocts, gastropods and crabs, France, **16,** 563 (*412*). Upper Carboniferous pygocephalomorph-syncarid assemblage, U.S.A., **19,** 411 (*486*). Early Miocene *in situ* hermit crab, New Zealand, **23,** 471 (*273*).

CYSTOIDEA

Ordovician Hemicosmitidae, Norway, Sweden, U.S.S.R., **22,** 363 (*61*).

ECHINOIDEA

Ecological interpretation of pore structures, **21,** 759 (*504*).

FORAMINIFERA

Pre-Miocene seagrass communities, Caribbean, **23,** 231 (*186*).

GASTROPODA

Symbiosis with Jurassic ectoprocts and crabs, France, **16,** 563 (*412*). Feeding habits of predatory Eocene assemblages, France, **13,** 254 (*534*). Succession and mode of life of Silurian faunas, Canada, **21,** 285 (*426*). Food specialization of predatory prosobranchs, **23,** 375 (*538*). Mode of life of giant Upper Cretaceous capulid, Japan, **23,** 689 (*248*).

OSTRACODA

Eocene assemblages and depositional environments, England, **20,** 405 (*301*).

PLANTAE

Lower Cretaceous debris beds, England, **19,** 437 (*399*). Upper Carboniferous assemblages, Scotland, **20,** 447 (*488*). Pre-Miocene seagrass communities, Caribbean, **23,** 231 (*186*). *Pseudofrenelopsis* and associated conifers, England, **24,** 759 (*11*).

POLLEN and SPORES

Lower Cretaceous soil beds, England, **16,** 399 (*48*).

TRILOBITA

Silurian faunas in pure limestones, **15,** 336 (*331*).

CAMBRIAN

Archaeocyathid-pseudostromatolite-*Renalcis* associations, Australia, **19,** 223 (*71*).

ORDOVICIAN

Caradoc marine benthic communities, Wales, **22,** 182 (*433*). Llanvirn benthic palaeocommunities, Wales, **24,** 661 (*595*). Ashgill regressive sequence, Norway, **25,** 783 (*72*).

SILURIAN

Wenlock-Ludlow marine communities, England and Wales, **17,** 779 (*92*). Ludlow benthic assemblages, England and Wales, **18,** 509 (*333*).

DEVONIAN

Saltern Cove Goniatite Bed, England, **15,** 430 (*568*).

MESOZOIC and TERTIARY

Hydroid-serpulid symbiosis, Europe and Middle East, **18,** 255 (*491*).

JURASSIC

Kimmeridgian palaeoenvironments, southern England, **16,** 261 (*79*). Bathonian hardground and crevice fauna, England, **17,** 507 (*410*). Callovian bituminous shale, England, **18,** 443 (*162*). Upper Jurassic marine benthic associations, England and France, **20,** 337 (*211*). Bathonian mammal bed, England, **22,** 135 (*209*). Bathonian carbonate lagoons, England, **22,** 189 (*409*). Bathonian sponge reefs, France, **24,** 1 (*411*).

CRETACEOUS

Ptychodus predation on *Inoceramus*, **15,** 439 (*298*). Aptian–Coniacian hiatus concretions and hardgrounds, South Africa, **15,** 539 (*312*). Isotopic ratios and Lower Cretaceous environments, England, **16,** 607 (*8*). Palaeoecology of Turonian *Scaphites* facies, Japan, **22,** 609 (*529*). Limpet grazing on Albian algal-bored ammonites, England, **25,** 361 (*4*). Fossil forests, Antarctica, **25,** 681 (*283*).

PLIOCENE

Palaeobiology of Coralline Crag Bryozoa, England, **25,** 529 (*35*).

PLEISTOCENE

Molluscan assemblages and faunal response to reef habitat instability, Indian Ocean, **21,** 1 (*536*).

RECENT

Coralline algal gravels, Ireland, **22,** 449 (*63*).

Palaeogeography

SILURIAN

Implications of Wenlock shelly faunas, Ireland, **18,** 343 (*586*).

JURASSIC

Regional changes across Lower Jurassic stage-boundary, Britain, **15,** 125 (*494*). Bathonian carbonate lagoons, England, **22,** 182 (*409*).

CRETACEOUS

Fossil forests, Antarctica, **25,** 681 (*283*).

Palynology

See Fungi, Microplankton, Pollen and Spores

Parablastoidea

ORDOVICIAN

Oldest known species, Arenig, Wales, **25,** 499 (*422*).

Pisces

GENERAL

Growth and form of finspines in hybodont sharks, **21,** 657 (*361*).

SILURIAN

Přídolí ostracoderm fauna, Canada, **19,** 1 (*342*). New Downton *Corvaspis*, Canada, **19,** 757 (*341*). Ludlow–Přídolí ostracoderms, Canada, **20,** 661 (*343*).

DEVONIAN

Gedinnian ostracoderm fauna, Canada, **19,** 1 (*342*). New Siegenian pteraspidid ostracoderm, Wales, **23,** 287 (*344*). New Emsian lungfish species, Australia, **25,** 509 (*94*). Sharks, Australia and Antarctica, **25,** 817 (*608*). New articulated thelodont, England, **25,** 879 (*567*).

CARBONIFEROUS

Jaw suspension in Pennsylvanian anacanthous sharks, U.S.A., **18,** 333 (*609*). Non-autostylic Pennsylvanian iniopterygians, U.S.A., **23,** 315 (*516*). Visēan shark *Onychoselache*, Scotland, **23,** 363 (*157*). Namurian–Westphalian coelacanth *Rhabdoderma*, British Isles, **24,** 203 (*200*). New Mississippian actinopterygian, U.S.A., **25,** 485 (*349*).

PERMIAN

Pleromic dentine in crossopterygian *Ectosteorhachis*, **19,** 749 (*553*).

TRIASSIC

Scythian–Ladinian chondrosteans, South Africa and Australia, **18,** 613 (*271*). Scythian redfieldiiform *Helichthys*, South Africa, **21,** 881 (*272*). New shark genus, Switzerland, **25,** 399 (*460*).

JURASSIC

New Liassic holosteans, India, **16,** 149 (*281*). Kimmeridgian selachian *Protospinax*, Germany, **19,** 733 (*360*). Dentition of Callovian chimaeroid *Brachymylus*, England, **20,** 589 (*576*).

CRETACEOUS

Neocomian–Cenomanian otoliths, England, **16,** 293 (*521*).

EOCENE

New scyliorhynid shark teeth, England, **20,** 195 (*96*). New species of *Amia*, Canada, **25,** 413 (*597*).

Plantae

GENERAL

Stratigraphic occurrence of early land plants, **15,** 365 (*36*). Scanning electron microscopy of latex casts, **16,** 645 (*98*). Interrelationships with early terrestrial arthropods, **18,** 391 (*320*). History of seagrass communities, **18,** 681 (*70*). Pre-Miocene seagrass communities, Caribbean, **23,** 231 (*186*).

SILURIAN

Fertile Downton Rhyniophytina, Wales, **13,** 451 (*166*). Downton terrestrial flora, Wales, **22,** 23 (*168*).

DEVONIAN

Fertile Ditton Rhyniophytina, Scotland, **13,** 451 (*166*). Cortical tissues of lycopod stem, **14,** 1 (*18*). Gedinnian–Siegenian flora, England, **17,** 311 (*169*). New heterosporous form, Canada, **17,** 387 (*17*). Non-vascular land flora, Ghana, **17,** 925 (*100*). Emsian flora, England, **21,** 693 (*99*). New Emsian zosterophyll, Poland, **25,** 247 (*610*). *Reimannia* and the Class Progymnospermopsida, U.S.A., **25,** 605 (*520*).

CARBONIFEROUS

Structure of Pennsylvanian *Cordaites*, North America, **13,** 29 (*223*). Epidermal studies of Westphalian *Lepidodendron*, **13,** 145 (*548*). New lycopods, Ghana, **14,** 357 (*375*). Female fructifications, Brazil and Australia, **15,** 108 (*461*). Namurian–Westphalian lepidodendroid stoma, Scotland, **17,** 525 (*549*). New Mississippian lycopod *Protostigmaria*, U.S.A., **18,** 19 (*290*). New Pennsylvanian pteropsid fructification, U.S.A., **19,** 307 (*471*). Westphalian plant debris in coprolites, England, **20,** 59 (*487*). Epidermis of Westphalian *Lepidophloios*, **20,** 273 (*550*). Ecology of Westphalian assemblages, Scotland, **20,** 447 (*488*). New Pennsylvanian marattialean fern, U.S.A., **21,** 709 (*291*). Pennsylvanian plant-bearing coprolites in coal balls, U.S.A., **22,** 537 (*49*). Fertile Pennsylvanian *Pecopteris*, U.S.A., **22,** 913 (*292*). Petrified Westphalian fern sporangium, England, **24,** 483 (*222*). Stem of Pennsylvanian pteridosperm *Medullosa*, U.S.A., **24,** 647 (*511*).

Plantae (*cont.*):

PERMIAN

New Upper Permian genus of osmundacean tree, Australia, **13,** 10 (*224*). Lower Gondwana female fructifications, Brazil and Australia, **15,** 108 (*461*).

TRIASSIC

Rhaetian flora, northern France, **13,** 433 (*390*). *Dinophyton*, new problematical genus, U.S.A., **13,** 646 (*23*). *Marcouia*, new problematical genus, U.S.A., **15,** 423 (*24*). Late Triassic flora, U.S.A., **15,** 598 (*25*). Unusual bennettitalean leaf, U.S.A., **20,** 641 (*26*). New species of the lycopsid *Pleuromeia*, China, **25,** 215 (*575*).

JURASSIC

Liassic flora, northern France, **13,** 433 (*390*). Kimmeridgian–Portlandian gymnospermous wood, Scotland and England, **15,** 655 (*144*). Bajocian *Williamsoniella* and its pollen, England, **17,** 125 (*245*). Portlandian (Purbeck) land plants and Charales, England, **18,** 419 (*37*). Succession of floras, U.S.S.R., **19,** 627 (*159*). Oxfordian araucarian cone, England, **23,** 657 (*522*).

CRETACEOUS

Maastrichtian staminate heads with pollen grains, U.S.S.R., **16,** 41 (*326*). Leaf anatomy of fusainized *Weichselia*, England, **17,** 587 (*9*). Lower Cretaceous plant debris beds, England, **19,** 437 (*399*). Rubber casts of silicified floras, Sudan, **19,** 641 (*580*). Cenomanian–Senonian conifers *Frenelopsis* and *Manica*, Portugal, **20,** 387 (*10*). Berriasian–Albian cheirolepidiacean conifers, U.S.A. and England, **20,** 715 (*579*). Preservation of leaf impressions, U.S.A., **20,** 907 (*515*). Barremian *Classopollis*-bearing male cone associated with *Pseudofrenelopsis*, England, **21,** 847 (*13*). Hauterivian–Barremian conifer *Frenelopsis* with opposite decussate leaves, Portugal, **21,** 873 (*12*). Late Cretaceous gymnosperms and the terminal Cretaceous event, U.S.S.R., **21,** 893 (*328*). Anatomy and palaeoecology of *Pseudofrenelopsis* and other Barremian conifers, England, **24,** 759 (*11*). Fossil forests, Antarctica, **25,** 681 (*283*).

PALAEOCENE

Danian staminate heads with pollen grains, U.S.S.R., **16,** 41 (*326*). Danian *Podocarpus*, eastern U.S.S.R., **17,** 365 (*327*).

EOCENE

Platanus wood, England, **15,** 496 (*73*). *In situ* Bartonian coniferous trees, England, **16,** 205 (*207*). Evolution of charophyte floras, England, **20,** 143 (*194*).

OLIGOCENE

Evolution of charophyte floras, England, **20,** 143 (*194*).

Pollen and Spores

GENERAL

Stereoscan observations on Triassic–Cretaceous *Classopollis*, **13,** 303 (*451*). Transmission electron microscopy, **16,** 787 (*304*).

DEVONIAN

Gedinnian–Siegenian assemblages, England, **17,** 311 (*169*). New heterosporous plant, Canada, **17,** 387 (*17*). Emsian *in situ* spores, England, **21,** 687 (*99*). Givetian miospores, Scotland, **25,** 277 (*364*).

CARBONIFEROUS

Ontogeny of Pennsylvanian *Vesicaspora*, **14,** 431 (*234*). Compression structures in Viséan miospore *Dictyotriletes*, Scotland, **15,** 121 (*114*). Transmission and scanning electron microscopy of *in situ* Pennsylvanian spores, U.S.A., **16,** 765 (*543*).

TRIASSIC

New Norian–Karnian *Ricciisporites*, Canada, **20,** 581 (*195*). Evolutionary sequence in *Aratrisporites* miospores, Australia, **25,** 665 (*155*).

JURASSIC

Bajocian *Williamsoniella* and compression of spherical pollen grains, England, **17,** 125 (*245*). Miospore assemblages, U.S.S.R., **19,** 627 (*159*). Bajocian–Bathonian assemblages, Norway, **21,** 31 (*56*).

CRETACEOUS

Swan River Group assemblages, Canada, **14,** 533 (*435*). Palynological assemblages in Wealden correlation, England, **16,** 1 (*47*). Maastrichtian–Danian staminate heads with pollen grains, U.S.S.R., **16,** 41 (*326*). Valanginian soil beds, England, **16,** 399 (*48*). Berriasian–Aptian correlation, England, **16,** 567 (*267*). Albian–Cenomanian angiosperm assemblages, England and France, **18,** 775 (*330*). Lower Cretaceous plant debris beds, England, **19,** 437 (*399*). Barremian *Classopollis*-bearing male cone associated with *Pseudofrenelopsis*, England, **21,** 847 (*13*). Barremian earliest angiosperm pollen, England, **22,** 513 (*268*).

TERTIARY

System of group names for pollen, **20,** 559 (*64*).

PALAEOCENE

Salviniacean massulae, England, **19,** 173 (*365*).

EOCENE

New multiple-floated *Azolla*, England, **23,** 213 (*124*).

OLIGOCENE

Megaspores and massulae of *Azolla*, England, **18,** 483 (*206*).

Porifera

CAMBRIAN

Dalradian *Protospongia*, Ireland, **16,** 231 (*476*).

CARBONIFEROUS

Sclerosponge affinities and spicule pseudomorphs in new Dinantian chaetetid, Wales, **23,** 803 (*230*).

JURASSIC

Ecology of Bathonian reefs, France, **24,** 1 (*411*).

CRETACEOUS

New Aptian sclerosponge, Czechoslovakia, **17,** 341 (*299*).

Preservation of fossils

Exceptional preservation in Middle Jurassic cyclostomatous bryozoans, England, **16,** 219 (*574*). Compression of Jurassic spherical pollen grains, England, **17,** 125 (*245*). Pre-depositional formation of leaf impressions, **20,** 907 (*515*). Colour markings on Lower Jurassic ammonite, England, **20,** 913 (*363*). Early Devonian plants, England, **21,** 687 (*99*). Red alga *Solenopora*, England, **25,** 905 (*244*).

Problematica

PRECAMBRIAN

Chuaria, U.S.A., **16,** 535 (*199*).

CAMBRIAN

Atdabanian lapworthellids, England, **16,** 139 (*369*). New lophophorate interpreted as conodontophorid, Canada, **19,** 199 (*125*). Atdabanian–Botomian *Renalcis*–archaeocyathid–pseudostromatolite associations, Australia, **19,** 223 (*71*). New metazoan, Canada, **20,** 623 (*126*). Atdabanian button-shaped phosphatic microfossils, U.S.S.R., **20,** 751 (*50*). New entoproct-like organism, Canada, **20,** 833 (*127*).

SILURIAN

New Llandovery microfossils, Norway and Sweden, **17,** 707 (*332*). Enigmatic metazoan, Sweden, **24,** 195 (*105*).

CRETACEOUS

Cretacicrusta, new possible alga, England, **15,** 501 (*176*).

R

Reefs

CAMBRIAN

Archaeocyathan faunas, Canada, **24,** 343 (*156*).

JURASSIC

Ecology of Bathonian sponge reefs, France, **24,** 1 (*411*).

PLEISTOCENE

Molluscan assemblages and faunal response to habitat instability, Indian Ocean, **21,** 1 (*536*). Succession and diversity in coral reefs, Kenya, **23,** 1 (*141*). Ecological stratification, Kenya, **24,** 609 (*142*).

Reptilia

GENERAL

Faunal replacement on Permo-Triassic continents, **14,** 131 (*464*).

PERMIAN

Autunian pelycosaurs, England, **17,** 541 (*418*). Oldest known millerettid, South Africa, **24,** 379 (*552*).

TRIASSIC

New dicynodonts, India, **13,** 132 (*107*). Skull of ornithischian dinosaur *Fabrosaurus*, Lesotho, **13,** 414 (*554*). Post-cranial skeleton of ornithischian dinosaur *Fabrosaurus*, Lesotho, **15,** 29 (*555*). Tooth function and succession in *Procolophon*, **20,** 695 (*227*). Primitive Carnian–Norian parasuchid, India, **21,** 83 (*103*). New rhynchocephalian, England, **25,** 709 (*208*).

JURASSIC

Lower Volgian pliosaur *Liopleurodon*, U.S.S.R., **14,** 566 (*235*). Bajocian megalosaurids, England, **17,** 325 (*571*). Hypsilophodontid dinosaurs, England, **18,** 741 (*217*). Bathonian–Tithonian dinosaur, England and U.S.A., **19,** **587** (*218*). Affinities of Liassic and later ichthyosaurs, **22,** 921 (*20*). Kimmeridgian ornithischian dinosaur *Camptosaurus*, England, **23,** 411 (*219*). Liassic plesiosaur embryos reinterpreted as shrimp burrows, England, **25,** 351 (*556*). Osteology of the Kimmeridgian lizard *Ardeosaurus*, Germany, **25,** 461 (*367*).

CRETACEOUS

Cenomanian chelonian *Rhinochelys*, England and France, **13,** 355 (*119*). Cranial morphology of new Purbeckian turtle, England, **18,** 25 (*187*). Hypsilophodontid dinosaurs, England, **18,** 741 (*217*). New Purbeckian turtle skull, England and early dichotomies of cryptodires, **19,** 317 (*188*). Giant mesosuchian crocodile *Sarcosuchus*, Brazil and Niger, **20,** 203 (*89*). Families of the ornithischian dinosaur Order Ankylosauria, **21,** 143 (*129*). Wealden crocodilian *Bernissartia*, England, **22,** 905 (*88*). Juveniles of the ornithischian dinosaur *Psittacosaurus*, Mongolia, **25,** 89 (*130*).

EOCENE

New Cuisian trionychid turtle, England, **13,** 503 (*383*). New Ypresian trionychid turtle, England, **17,** 901 (*572*).

MIOCENE

New crocodiles, Kenya, **21,** 857 (*544*).

S

Scaphopoda

JURASSIC

New Callovian species, England, **18,** 377 (*408*).

Scyphozoa

PRECAMBRIAN

Ediacaran fauna, Australia, **15,** 197 (*570*).

Shell structure

See Ultrastructure.

Somasteroidea

Morphology and relationships, **25,** 167 (*60*).

Stratigraphy

GENERAL

Automatic production of range-diagrams, **17,** 553 (*428*).

CAMBRIAN

Idamean biostratigraphy and correlation, Australia, **19,** 325 (*250*).

ORDOVICIAN

Ashgill biostratigraphy and the *Hirnantia* fauna, Wales, **18,** 703 (*118*). Champlainian–Cincinnatian conodont and graptolite biostratigraphy, U.S.A. **21,** 723 (*52*). Tremadoc graptolite sequence, Australia, **22,** 767 (*133*).

SILURIAN

Wenlock Series, England and Wales, **17,** 745 (*40*). Llandovery biostratigraphy, Wales, **18,** 703 (*118*).

DEVONIAN

Eifelian–Famennian conodont biostratigraphy, England, **21,** 907 (*400*).

CARBONIFEROUS

Dinantian conodont correlations, England, **17,** 371 (*373*). Dinantian conodont biostratigraphy, Australia, **17,** 909 (*288*).

Stratigraphy (*cont.*):

JURASSIC

Bajocian–Volgian biostratigraphy, Norway, **21,** 31 (*56*). Kimmeridgian ammonites and stratigraphy, England, **21,** 469 (*134*). *Amoeboceras* zonation of Boreal upper Oxfordian, **22,** 839 (*528*).

CRETACEOUS

Ryazanian–Valanginian biostratigraphy, Norway, **21,** 31 (*56*).

OLIGOCENE

Foraminiferal biostratigraphy, Indian Ocean, **17,** 475 (*1*).

MIOCENE

Foraminiferal biostratigraphy, Indian Ocean, **17,** 475 (*1*).

Stromatolites

PRECAMBRIAN

Periodicities in lamination of Proterozoic forms, Canada, **24,** 231 (*296*).

TRIASSIC

Rhaetian algal tuft structures, England, **24,** 655 (*374*).

See also Algae.

Stromatoporoidea

ORDOVICIAN

Alleynodictyon new genus, Australia, **14,** 10 (*581*).

DEVONIAN

Givetian–Frasnian *Amphipora* and *Euryamphipora*, Canada, **13,** 64 (*198*). Reinterpretation of alga *Keega* as basal layer, Canada and Australia, **17,** 565 (*454*).

T

Techniques

Use of the pictograph, **15,** 378 (*164*). Use of palynological biorecords in correlation, **16,** 567 (*267*). Scanning electron microscopy of latex casts of plants, **16,** 645 (*98*). Application of electron microscopy, **16,** 733 (*391*). Improved method of mounting specimens for SEM examination, **17,** 431 (*197*). Specimen location on SEM strew mounts, **17,** 435 (*329*). Automatic production of stratigraphical range diagrams, **17,** 553 (428). Production of faunal lists by automatic methods, **18,** 865 (*429*). Analogue Video Reshaper for deformed fossils, **19,** 565 (*21*). Silicone rubber casts of silicified plants, **19,** 641 (*580*). Reconstruction of internal structures of micromorphic fossils, **21,** 463 (*31*). Biorecords and SEM examination of Lower Cretaceous pollen, England, **22,** 513 (*268*). Preparation of stereom structures in crinoids, **23,** 749 (*497*). Outline processing in biometry and systematics, **23,** 757 (*497*). Floating orientations of cephalopod shell models, **23,** 931 (*450*). Generating curve of straight-hinged bivalves, **25,** 109 (*446*). Bone recovery from sediment residues, **25,** 471 (*210*).

See also Biometrics.

Teuthoidea

Cenozoic statoliths, U.S.A., **22,** 479 (*108*).

Trace fossils

GENERAL

Fossil and Recent echinoid bioerosion, **18,** 725 (*78*).

CAMBRIAN

Habits of the trilobite *Olenoides*, Canada, **23,** 171 (*593*).

SILURIAN

Llandovery *Dictyodora*, Scotland, **23,** 501 (*51*).

CARBONIFEROUS

New Namurian xiphosurid trails, England, **13,** 188 (*239*). Westphalian coprolites containing plant debris, England, **20,** 59 (*487*). Namurian giant myriapod trail, Scotland, **22,** 273 (*77*). Pennsylvanian plant-bearing coprolites in coal balls, U.S.A., **22,** 537 (*49*).

PERMIAN

Fish trails, South Africa, **19,** 397 (*15*).

TRIASSIC

Comparison of invertebrate traces, England and Germany, **24,** 555 (*438*).

JURASSIC

Thalassinoides burrow containing crustacean, England, **14,** 589 (*493*). Liassic plesiosaur embryos reinterpreted as shrimp burrows, England, **25,** 351 (*556*).

CRETACEOUS

Thallophyte borings in phosphatic fossils, Antarctica, **14,** 294 (*533*). Albian hydrozoan *Kirklandia* revised as trace fossil, U.S.A., **18,** 665 (*213*). Late Cretaceous fish coprolites, Canada, **21,** 443 (*80*). Limpet grazing on Albian algal-bored ammonites, England, **25,** 361 (*4*).

Trilobita

GENERAL

Statistical analysis of trinucleid fringes, **13,** 1 (*265*). Nature of cuticle, **21,** 459 (*559*). Visual system, **22,** 1 (*111*).

CAMBRIAN

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Fertile Ditton Rhyniophytina, Scotland, **13,** 451 (*166*). Cortical tissues of lycopod stem, **14,** 1 (*18*). Early land floras, **15,** 365 (*36*). Gedinnian-Siegenian flora, England, **17,** 311 (*169*). New heterosporous form, Canada, **17,** 387 (*17*). Non-vascular land flora, Ghana, **17,** 925 (*100*). Emsian flora, England, **21,** 693 (*99*). New Emsian zosterophyll, Poland, **25,** 247 (*610*). *Reimannia* and the Class Progymnospermopsida, U.S.A., **25,** 601 (*520*).

POLLEN and SPORES

Gedinnian-Siegenian assemblages, England, **17,** 311 (*169*). New heterosporous plant, Canada, **17,** 387 (*17*). Emsian *in situ* spores, England, **21,** 693 (*99*). Givetian miospores, Scotland, **25,** 277 (*364*).

STRATIGRAPHY

Eifelian-Famennian conodont biostratigraphy, England, **21,** 907 (*400*).

STROMATOPOROIDEA

Givetian-Frasnian *Amphipora* and *Euryamphipora*, Canada, **13,** 64 (*198*). Reinterpretation of alga *Keega* as basal layer, Canada and Australia, **17,** 565 (*454*).

TRILOBITA

Lochkovian fauna, Czechoslovakia, **14,** 159 (*106*). New Eifelian-Givetian *Phacops*, Mauritania and Morocco, **17,** 349 (*90*). Classification and phylogeny of homalonotids, **20,** 159 (*546*). Review of Aulacopleuridae, **21,** 65 (*547*). Lochkovian-Pragian fauna, Australia, **22,** 799 (*104*). Phacopid sculpture and microstructure, Poland, **23,** 237 (*525*).

Carboniferous

ALGAE

New Viséan calcareous taxa, England and Wales, **13,** 443 (*173*). Ultrastructure and diagenesis of Viséan *Koninckopora*, Wales, **24,** 185 (*607*).

AMMONOIDEA

Dimorphic Namurian goniatite, England, **13,** 40 (*561*). New Tournaisian goniatite fauna, England, **13,** 112 (*368*). Tournaisian-Viséan faunas and biostratigraphy, Spain, **25,** 313 (*254*).

AMPHIBIA

Primitive Viséan labyrinthodont *Crassigyrinus*, Scotland, **16,** 179 (*413*). Westphalian temnospondyl *Dendrerpeton*, Ireland, **23,** 125 (*381*). Pennsylvanian edopoid labyrinthodont *Cochleosaurus*, Canada, **23,** 143 (*459*). New Viséan-Namurian labyrinthodont, Scotland, **23,** 915 (*510*). Axial skeleton of Westphalian *Pteroplax*, England, **23,** 273 (*65*). Westphalian lysorophid, England, **23,** 925 (*66*). Jaw ramus of Westphalian *Anthracosaurus*, England, **24,** 85 (*414*). New Viséan aïstopod, Scotland, **25,** 193 (*587*). Westphalian aïstopod *Ophiderpeton*, England, **25,** 209 (*67*). Pennsylvanian temnospondyls, U.S.A., **25,** 635 (*382*).

ANTHOZOA

Orionastraea, new Viséan rugose genus, England, **13,** 47 (*297*). Variation in Viséan *Caninia*, Ireland, **13,** 52 (*158*). Distribution and growth of Viséan caninioids, Ireland, **13,** 191 (*263*). Coiled protocoralla in Mississippian rugosan *Cyathaxonia*, U.S.A., **20,** 47 (*481*).

ARACHNIDA

New Westphalian species, England, **15,** 569 (*14*).

BIOGEOGRAPHY

Ectoproct Bryozoa, **24,** 313 (*470*).

BLASTOIDEA

Viséan fissiculate forms, Scotland, **20,** 225 (*358*).

BRACHIOPODA

Viséan endopunctate rhynchonellid, England, Wales, Ireland, Belgium, **14,** 95 (*83*). Viséan fauna, England, **17,** 811 (*85*). Tournaisian-Stephanian? chonetaceans and productaceans, Australia, **19,** 17 (*463*). Micro-ornamentation of Viséan spiriferides, Ireland, **19,** 767 (*84*). New Bashkirian-Moscovian stenoscismataceans, Spain, **20,** 209 (*366*).

BRYOZOA

Viséan *Polypora* with cheilostomatous features, **14,** 178 (*530*). Early growth in Tournaisian rhabdomesoids, Ireland, **17,** 149 (*531*). New Tournaisian-Stephanian problematical form, Australia, **18,** 571 (*185*). Ectoproct biogeography, **24,** 313 (*470*).

CONODONTOPHORIDA

Dinantian fauna, England, **15,** 550 (*372*). Tournaisian faunas, Ireland, **16,** 335 (*371*). Tournaisian-Viséan faunas, England, **16,** 477 (*91*). Dinantian faunas, England, **17,** 371 (*373*). Dinantian biostratigraphy, Australia, **17,** 909 (*288*). Namurian faunas, Malaysia, **23,** 297 (*376*). Westphalian coprolitic assemblages, England, **24,** 437 (*252*). Dinantian faunas, England, **25,** 145 (*253*). Tournaisian-Viséan faunas and biostratigraphy, Spain, **25,** 313 (*254*).

CRINOIDEA

Technique for revealing stereom structure, **23,** 749 (*497*).

CRUSTACEA

Pennsylvanian pygocephalomorph-syncarid assemblage, U.S.A., **19,** 411 (*486*).

INSECTA

Westphalian palaeodictyopteran nymphs, England, **15,** 662 (*598*).

MEROSTOMATA

New Westphalian xiphosurid, England, **15,** 569 (*14*). Westphalian eurypterid, Wales, **19,** 185 (*403*).

MYRIAPODA

Trail of giant Namurian *Arthropleura*, Scotland, **22,** 273 (*77*).

NAUTILOIDEA

New fauna, Argentina, **18,** 117 (*452*).

OSTRACODA

New Viséan podocopine? family, U.S.S.R., **20,** 475 (*228*).

PALAEOECOLOGY

Pennsylvanian pygocephalomorph–syncarid assemblage, U.S.A., **19,** 411 (*486*). Westphalian plant assemblages, Scotland, **20,** 447 (*488*).

PISCES

Jaw suspension in Pennsylvanian anacanthous sharks, U.S.A., **18,** 333 (*609*). Non-autostylic Pennsylvanian iniopterygians, U.S.A., **23,** 315 (*516*). Viséan shark *Onychoselache*, Scotland, **23,** 363 (*157*). Namurian–Westphalian coelacanth *Rhabdoderma*, British Isles, **24,** 203 (*200*). New Mississippian actinopterygian, U.S.A., **25,** 485 (*349*).

PLANTAE

Structure of Pennsylvanian *Cordaites*, North America, **13,** 29 (*223*). Epidermal studies of Westphalian *Lepidodendron*, **13,** 145 (*548*). New lycopods, Ghana, **14,** 357 (*375*). Female fructifications, Brazil and Australia, **15,** 108 (*461*). Namurian–Westphalian lepidodendroid stoma, Scotland, **17,** 525 (*549*). New Mississippian lycopod *Protostigmaria*, U.S.A., **18,** 19 (*290*). New Pennsylvanian pteropsid fructification, U.S.A., **19,** 307 (*471*). Westphalian plant debris in coprolites, England, **20,** 59 (*487*). Epidermis of Westphalian *Lepidophloios*, **20,** 273 (*550*). Ecology of Westphalian assemblages, Scotland, **20,** 447 (*488*). New Pennsylvanian marattialean fern, U.S.A., **21,** 709 (*291*). Pennsylvanian plant-bearing coprolites in coal balls, U.S.A., **22,** 537 (*49*). Fertile Pennsylvanian *Pecopteris*, U.S.A., **22,** 913 (*292*). Petrified Westphalian fern sporangium, England, **24,** 483 (*222*). Stem of Pennsylvanian pteridosperm *Medullosa*, U.S.A., **24,** 647 (*511*).

POLLEN and SPORES

Ontogeny of Pennsylvanian *Vesicaspora*, **14,** 431 (*234*). Compression structures in Viséan miospore *Dictyotriletes*, Scotland, **15,** 121 (*114*). Transmission and scanning electron microscopy of *in situ* Pennsylvanian spores, U.S.A., **16,** 765 (*543*).

PORIFERA

Sclerosponge affinities and spicule pseudomorphs in new Dinantian chaetitid, Wales, **23,** 803 (*230*).

STRATIGRAPHY

Dinantian conodont correlations, England, **17,** 371 (*373*). Dinantian conodont biostratigraphy, Australia, **17,** 909 (*288*).

TRACE FOSSILS

New Namurian xiphosurid trails, England, **13,** 188 (*239*). Westphalian coprolites containing plant debris, England, **20,** 59 (*487*). Namurian giant myriapod trail, Scotland, **22,** 273 (*77*). Pennsylvanian plant-bearing coprolites in coal balls, U.S.A., **22,** 537 (*49*).

TRILOBITA

Viséan fauna, Ireland, **16,** 391 (*232*). Viséan fauna, England, **16,** 551 (*233*). Synonymy of Viséan *Namuropyge* and *Coignouina*, England, **20,** 917 (*379*). Review of Aulacopleuridae, **21,** 65 (*547*).

Permian

ALGAE

?Artinskian–Kungurian Codiaceae, Iraq and Oman, **13,** 327 (*172*). Nature of *Aciculella*, Italy, **14,** 629 (*174*).

AMPHIBIA

Autunian temnospondylous labyrinthodont, England, **18,** 831 (*419*). Autunian labyrinthodonts, *Menonomenos* and *Cricotillus*, Czechoslovakia and U.S.A., **21,** 667 (*380*).

ANTHOZOA

Tetracorals, *Lophophyllidium* and *Timorphyllum*, U.S.A., **17,** 441 (*192*). Coloniality in Wolfcampian rugosan *Heritschioides*, U.S.A., **21,** 177 (*193*). Structure and composition of Guadalupian rugosans, Indonesia, **21,** 321 (*513*).

BIVALVIA

Bizarre new myalinid, Malaysia and Japan, **18,** 315 (*474*).

BRYOZOA

Zoarial microstructure of *Stenopora*, **13,** 581 (*22*). Ectoproct biogeography, **21,** 341 (*469*).

CONODONTOPHORIDA

Derived and indigenous elements, England, **25,** 845 (*527*).

FORAMINIFERA

Morphological variation in Wolfcampian *Schwagerina*, U.S.A., **13,** 175 (*480*).

INSECTA

Heads of Homoptera, Australia, **14,** 211 (*457*).

OSTRACODA

New Asselian podocopid and its muscle-scar field, U.S.S.R., **18,** 551 (*229*).

PISCES

Pleromic dentine in crossopterygian *Ectosteorhachis*, **19,** 749 (*553*).

PLANTAE

New Upper Permian genus of osmundacean tree, Australia, **13,** 10 (*224*). Lower Gondwana female fructifications, Brazil and Australia, **15,** 108 (*461*).

REPTILIA

Faunal replacement on continents, **14,** 131 (*464*). Autunian pelycosaurs, England, **17,** 541 (*418*). Oldest known millerettid, South Africa, **24,** 379 (*552*).

TRACE FOSSILS

Fish trails, South Africa, **19,** 397 (*15*).

TRILOBITA

New proetids, Australia, **14,** 222 (*578*).

Triassic

ALGAE

Tuff structures in Rhaetian stromatolites, England, **24,** 655 (*374*).

AMMONOIDEA

Preservational history of ceratite shells, **14,** 16 (*492*). Shell structure, **15,** 637 (*560*).

AMPHIBIA

New capitosaurid labyrinthodont, East Africa, **13,** 210 (*262*). Ladinian capitosauroid labyrinthodonts, England, **17,** 253 (*417*). Replacement name for labyrinthodont *Parotosaurus*, Germany, **19,** 415 (*420*).

Triassic (*cont.*):

ANTHOZOA

Structure and composition of Carnian scleractinians, Italy, **21,** 321 (*513*).

CONODONTOPHORIDA

Carnian faunas, Sumatra, **22,** 737 (*377*).

MICROPLANKTON

Rhaetian dinoflagellate *Rhaetogonyaulax*, England and Austria, **18,** 847 (*243*).

PISCES

Scythian–Ladinian chondrosteans, South Africa and Australia, **18,** 613 (*271*). Scythian redfieldiiform *Helichthys*, South Africa, **21,** 881 (*272*). New shark genus, Switzerland, **25,** 399 (*460*).

PLANTAE

Rhaetian flora, northern France, **13,** 433 (*390*). *Dinophyton*, new problematical genus, U.S.A., **13,** 646 (*23*). *Marcouia*, new problematical genus, U.S.A., **15,** 423 (*24*). Late Triassic flora, U.S.A., **15,** 598 (*25*). Unusual bennettitalean leaf, U.S.A., **20,** 641 (*26*). New species of the lycopsid *Pleuromeia*, China, **25,** 215 (*575*).

POLLEN and SPORES

Stereoscan observations on *Classopollis*, **13,** 303 (*451*). New Norian–Karnian *Ricciisporites*, Canada, **20,** 581 (*195*). Evolutionary sequence in *Aratrisporites* miospores, Australia, **25,** 665 (*155*).

REPTILIA

New dicynodonts, India, **13,** 132 (*107*). Skull of ornithischian dinosaur *Fabrosaurus*, Africa, **13,** 414 (*554*). Faunal replacement on continents, **14,** 131 (*464*). Post-cranial skeleton of ornithischian dinosaur *Fabrosaurus*, Lesotho, **15,** 29 (*555*). Tooth function and succession in *Procolophon*, **20,** 695 (*227*). Primitive Carnian–Norian parasuchid, India, **21,** 83 (*103*). New rhynchocephalian, England, **25,** 709 (*208*).

STROMATOLITES

Rhaetian algal tuft structures, England, **24,** 655 (*374*).

TRACE FOSSILS

Comparison of invertebrate traces, England and Germany, **24,** 555 (*438*).

Jurassic

ALGAE

Tethyan dasycladacean *Pseudocymopolia*, **13,** 323 (*171*). Ecology of transported Bathonian microflora, England, **18,** 351 (*179*). Taxonomy and opercular function of Bathonian–Bajocian *Stichoporella*, France and England, **22,** 407 (*183*). New Aalenian calcareous Chlorophyta, England, **25,** 431 (*184*). Bathonian *Solenopora*, England, **25,** 905 (*244*).

AMMONOIDEA

Wrinkle-layer structures, **14,** 107 (*495*). Type material of *Macrocephalites*, **14,** 114 (*93*). Bajocian fauna, Scotland, **14,** 266 (*386*). Jaws, radula and crop of Liassic *Arnioceras*, England, **14,** 338 (*334*). Bajocian *Dorsetensia*, Scotland, **15,** 504 (*387*). Aptychi of Bajocian *Sonninia*, Scotland, **16,** 195 (*388*). Bajocian Sonniniidae and other faunas, Scotland, **18,** 41 (*389*). Upper Bajocian fauna, England, **18,** 191 (*415*). Lectotype of Bajocian *Cadomites*, France, **18,** 871 (*590*). Tethyan Toarcian *Meneghiniceras*, England, **19,** 773 (*260*). Bajocian microconch otoitids, Europe, **20,** 101 (*416*). Aalenian *Bredyia*, **20,** 675 (*496*). Colour markings on Sinemurian specimen, England, **20,** 913 (*363*). Kimmeridgian–Volgian faunas, Norway, **21,** 31 (*56*). Kimmeridgian faunas and stratigraphy, England, **21,** 469 (*134*). Jaws and radula of Liassic *Dactylioceras*, England and Germany, **22,** 265 (*335*). *Amoeboceras* zonation of Boreal Upper Oxfordian, **22,** 839 (*528*). Toarcian stratigraphy, England, **23,** 637 (*261*). Rare Pliensbachian lytoceratid, England, **25,** 439 (*160*).

BELEMNOIDEA

Morphology and taxonomy of Kimmeridgian '*Rhopaloteuthis*', Somalia, **15,** 158 (*284*).

BIVALVIA

New Domerian–Callovian genus ancestral to *Globocardium*, England, France, Tanzania, **17,** 165 (*407*). Bathonian euryhaline oyster, England and Scotland, **19,** 79 (*264*). Ecology of Volgian *Hiatella*, England, **23,** 769 (*302*). Antarctic inoceramids and their stratigraphical use, **25,** 555 (*143*). Buchiid faunas, Greenland, **25,** 727 (*526*). Bathonian–Oxfordian anomiid?, England and France, **25,** 897 (*214*).

BRACHIOPODA

Growth and microstructure of thecideacean *Moorellina*, England, **13,** 76 (*27*). Morphology and microstructure of *Zellania*, England, **13,** 606 (*28*). New Bajocian micromorphic rhynchonellide, England, **14,** 696 (*29*). Systematic position of *Cadomella*, **15,** 405 (*86*). Loop development in Aalenian *Zeilleria*, England, **15,** 450 (*30*). Terebratulide affinity of Bajocian *Spirifera minima*, England, **18,** 879 (*32*). Functional morphology and ontogeny of Bathonian *Septirhynchia*, Tunisia, **22,** 317 (*362*).

BRYOZOA

Exceptional preservation in Pliensbachian cyclostomes, England, **16,** 219 (*574*). Symbiosis between Bathonian ectoprocts, gastropods and crabs, France, **16,** 563 (*412*). Multilamellar growth in Bathonian cyclostomes, France and England, **19,** 293 (*539*). Bathonian *Terebellaria*, England and France, **21,** 357 (*540*). New Aalenian–Bajocian–Bathonian species, England, **23,** 699 (*541*). Portlandian fauna, England, **24,** 863 (*542*).

CRUSTACEA

Bathonian *Glyphaea* in *Thalassinoides* burrow, England, **14,** 589 (*493*).

DECAPODA

Symbiosis between Bathonian ectoprocts, gastropods and crabs, France, **16,** 563 (*412*).

ECHINOIDEA

Lantern morphology and phylogeny of post-Palaeozoic forms, **24,** 779 (*506*). Tooth structure of the pygasteroid *Plesiechinus*, England, **25,** 891 (*507*).

FORAMINIFERA

Volgian assemblages, Norway, **22,** 413 (*345*).

GASTROPODA

Symbiosis with Bathonian ectoprocts and crabs, France, **16,** 563 (*412*).

MALACOSTRACA

Cuticle ultrastructure of Callovian lobster *Eryma*, England, **14,** 201 (*397*).

MAMMALIA

Bathonian mammal bed, England, **22,** 135 (*209*).

MICROPLANKTON

Hettangian dinoflagellate *Rhaetogonyaulax*, England and Austria, **18,** 847 (*243*). Kimmeridgian–Volgian dinocysts, Norway, **21,** 31 (*56*). Bajocian–Bathonian dinoflagellates and acritarchs, England, **23,** 151 (*196*).

OSTRACODA

Lower Lias fauna, England, **14,** 642 (*346*). New Liassic genera *Wicherella* and *Gramannella*, England, **15,** 187 (*347*). Domerian–Toarcian faunas, England, **17,** 599 (*348*). Freshwater fauna, India, **18,** 207 (*226*). Portlandian (Purbeck) freshwater fauna, England, **18,** 419 (*37*).

PALAEOECOLOGY

Kimmeridgian palaeoenvironments, southern England, **16,** 261 (*79*). Symbiosis between Bathonian ectoprocts, gastropods and crabs, France, **16,** 563 (*412*). Bathonian hardground and crevice fauna, England, **17,** 507 (*410*). Habitats of transported Bathonian algae, England, **18,** 351 (*179*). Callovian bituminous shale, England, **18,** 443 (*162*). Corallian marine benthic associations, England and France, **20,** 337 (*211*). Bathonian mammal bed, England, **22,** 135 (*209*). Bathonian carbonate lagoons, England, **22,** 189 (*409*). Bathonian sponge reefs, France, **24,** 1 (*411*).

PALAEOGEOGRAPHY

Sinemurian–Pliensbachian regional environmental changes, Britain, **15,** 125 (*494*). Bathonian carbonate lagoons, England, **22,** 182 (*409*).

PISCES

New Liassic holosteans, India, **16,** 149 (*281*). Kimmeridgian selachian *Protospinax*, Germany, **19,** 733 (*360*). Dentition of Callovian chimaeroid *Brachymylus*, England, **20,** 589 (*576*).

PLANTAE

Liassic flora, northern France, **13,** 433 (*390*). Kimmeridgian–Portlandian gymnospermous wood, Scotland and England, **15,** 655 (*144*). Bajocian *Williamsoniella* and its pollen, England, **17,** 125 (*245*). Portlandian (Purbeck) land plants and Charales, England, **18,** 419 (*37*). Succession of floras, U.S.S.R., **19,** 627 (*159*). Oxfordian araucarian cone, England, **23,** 657 (*522*).

POLLEN and SPORES

Stereoscan observations on *Classopollis*, **13,** 303 (*451*). Bajocian *Williamsoniella* and compression of spherical pollen grains, England, **17,** 125 (*245*). Miospore assemblages, U.S.S.R., **19,** 627 (*159*). Bajocian–Bathonian assemblages, Norway, **21,** 31 (*56*).

PORIFERA

Ecology of Bathonian reefs, France, **24,** 1 (*411*).

REEFS

Ecology of Bathonian sponge reefs, France, **24,** 1 (*411*).

REPTILIA

Lower Volgian pliosaur *Liopleurodon*, U.S.S.R., **14,** 566 (*235*). Bajocian megalosaurids, England, **17,** 325 (*571*). Hypsilophodontid dinosaurs, England, **18,** 741 (*217*). Bathonian–Tithonian dinosaur, England and U.S.A., **19,** 587 (*218*). Affinities of Liassic and later ichthyosaurs, **22,** 921 (*20*). Kimmeridgian ornithischian dinosaur *Camptosaurus*, England, **23,** 411 (*219*). Liassic plesiosaur embryos reinterpreted as shrimp burrows, England, **25,** 351 (*556*). Osteology of the Kimmeridgian lizard *Ardeosaurus*, Germany, **25,** 461 (*367*).

SCAPHOPODA

New Callovian species, England, **18,** 377 (*408*).

STRATIGRAPHY

Bajocian–Volgian biostratigraphy, Norway, **21,** 31 (*56*). Kimmeridgian ammonites and stratigraphy, England, **21,** 469 (*134*). *Amoeboceras* zonation of Boreal Upper Oxfordian, **22,** 839 (*528*).

TRACE FOSSILS

Bathonian *Thalassinoides* burrow containing crustacean, England, **14,** 589 (*493*). Liassic plesiosaur embryos reinterpreted as shrimp burrows, England, **25,** 351 (*556*).

Cretaceous

ALGAE

Tethyan dasycladacean *Pseudocymopolia*, **13,** 323 (*171*). Valanginian–Hauterivian Codiaceae, Iraq, **13,** 327 (*172*). New Upper Cretaceous dasycladacean, Borneo, **15,** 619 (*177*).

AMMONOIDEA

Cenomanian *Acanthoceras*, France, **13,** 462 (*308*). Cenomanian *Mantelliceras* and the *martimpreyi* Zone, England, **14,** 437 (*309*). Upper Albian *Ptychoceras*, England, **14,** 592 (*255*). Santonian *Texanites–Spinaptychus* association, South Africa, **15,** 394 (*311*). Affinities of Albian *Idiohamites ellipticoides*, England, **15,** 400 (*305*). Cenomanian fauna, Germany, **15,** 445 (*238*). Status of genera proposed by C. Jacob in 1907, **17,** 727 (*259*). Barremian heteromorphs *Paracrioceras* and *Hoplocrioceras*, England, **18,** 275 (*447*). Hauterivian *Lyticoceras* and its synonym *Endemoceras*, England, France, Germany, **18,** 607 (*603*). New Albian carinate phylloceratid, South Africa, **18,** 657 (*324*). Albian micromorph *Falloticeras*, **20,** 793 (*307*). Cenomanian earliest tissotiid, England, **20,** 901 (*306*). Ryazanian–Valanginian faunas, Norway, **21,** 31 (*56*). Cenomanian *Stoliczkaia*, England and France, **21,** 393 (*605*). Palaeoecology of Turonian *Scaphites* facies, Japan, **22,** 609 (*529*). Type Turonian vascoceratids, France, **22,** 665 (*314*). Origin and evolution of Albian–Cenomanian micromorph Flickiidae, **22,** 685 (*606*). European Turonian species of *Romaniceras*, **23,** 325 (*317*). Turonian collignoniceratids, England and France, **23,** 557 (*318*). Origin, evolution and systematics of Turonian *Spathites*, **23,** 821 (*319*). Upper Cenomanian faunas, France, **24,** 25 (*310*). Tethyan ancestry of north-west European faunas, **24,** 251 (*303*). Last Cenomanian mortoniceratines, **24,** 417 (*315*). Type Turonian Desmocerataceae, France, **24,** 493 (*316*).

Cretaceous (*cont.*):

ANNELIDA

Aptian serpulids, England, **18,** 93 (*577*).

AVES

New Barremian humerus, England, **16,** 721 (*246*). New Maastrichtian owl family, Romania, **18,** 563 (*247*).

BELEMNOIDEA

Palaeobiology of Santonian-Campanian faunas, England and France, **23,** 889 (*282*). Diplobelinid faunas, England and France, **24,** 115 (*285*).

BIVALVIA

Aptian-Albian protocardiids, England, Tanzania, **17,** 165 (*407*). Ryazanian-Valanginian buchias, Norway, **21,** 31 (*56*). Buchiid faunas, Greenland, **25,** 727 (*526*).

BRACHIOPODA

Albian terebratulaceans, England, **21,** 411 (*139*). Aptian thecideidines, England, **21,** 555 (*33*). Maastrichtian shallow-water fauna, North Atlantic ocean, **23,** 463 (*191*). Berriasian-Aptian terebratulids, Morocco, **23,** 515 (*378*).

DECAPODA

Moults of Maastrichtian crab, *Dakoticancer*, U.S.A., **15,** 631 (*57*). New Campanian-Maastrichtian? retroplumid, Nigeria, **18,** 823 (*121*).

ECHINOIDEA

Santonian-Campanian sympatric species of *Micraster*, England, **19,** 689 (*523*). Turonian-Senonian *Micraster* and *Epiaster*, England, **20,** 805 (*524*). Palaeobiology of Senonian *Infulaster* and *Hagenowia*, England, **25,** 11 (*216*).

FORAMINIFERA

Unusual new Senonian agglutinating form, England, **16,** 637 (*3*). Maastrichtian faunas, Jordan, **19,** 517 (*215*). Evolution of Albian *Arenobulimina*, *Gavelinella* and *Hedbergella*, England, France, Netherlands, Germany, **20,** 503 (*443*). Ryazanian-Hauterivian assemblages, Norway, **22,** 413 (*345*). Maastrichtian arenaceous faunas, Nigeria, **22,** 947 (*431*). Senonian *Gavelinella*, England and France, **24,** 391 (*170*).

GASTROPODA

Mode of life of giant Campanian capulid, Japan, **23,** 689 (*248*).

HYDROZOA

Albian *Kirklandia* revised as trace fossil, U.S.A., **18,** 665 (*213*).

MEROSTOMATA

New freshwater xiphosuran genus, Australia, **14,** 206 (*458*).

MICROPLANKTON

Terminology for dinoflagellate walls, cavities and bodies, **14,** 22 (*140*). Campanian dinoflagellates and acritarchs, Canada, **16,** 665 (*240*). Type Aptian dinoflagellate cysts, France, **17,** 623 (*153*). Campanian?-Maastrichtian dinoflagellate cysts, U.S.A., **20,** 179 (*241*). Ryazanian-Valanginian dinocysts, Norway, **21,** 31 (*56*). New Barremian dinocysts, North Sea, **22,** 427 (*152*).

OSTRACODA

New taxa with phosphatized appendages, Brazil, **15,** 379A (*45*). Maastrichtian *Hornibrookella*, Saudi Arabia, **20,** 483 (*7*).

PISCES

Neocomian-Cenomanian otoliths, England, **16,** 293 (*521*).

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Middle Triassic capitosauroid labyrinthodonts, Warwickshire, Worcestershire, Staffordshire, Devonshire, **17,** 253 (*417*). Lower Permian temnospondylous labyrinthodont, Warwickshire, **18,** 831 (*419*). Axial skeleton of Upper Carboniferous *Pteroplax*, Northumberland, **23,** 273 (*65*). Upper Carboniferous lysorophid, Northumberland, **23,** 925 (*66*). Jaw ramus of Upper Carboniferous *Anthracosaurus*, Northumberland, **24,** 85 (*414*). Upper Carboniferous aïstopod *Ophiderpeton*, Northumberland, **25,** 209 (*67*).

ANNELIDA

Lower Cretaceous serpulids, **18,** 93 (*577*).

ANTHOZOA

New Lower Carboniferous rugosan, **13,** 47 (*297*). Silurian tabulate *Paleofavosites*, Welsh Borderland, **21,** 307 (*439*).

ARACHNIDA

New Upper Carboniferous species, Somerset, **15,** 569 (*14*).

AVES

New Lower Cretaceous humerus, Sussex, **16,** 721 (*246*).

BELEMNOIDEA

Palaeobiology of Upper Cretaceous faunas, Hampshire and Sussex, **23,** 889 (*282*). Lower Cretaceous diplobelinids, **24,** 115 (*285*).

BIVALVIA

Periodicity structures and growth in *Cerastoderma*, Thames Estuary, **14,** 571 (*189*), New Lower–Middle Jurassic genus ancestral to *Globocardium*, *Somerset*, **17,** 165 (*407*). Lower Cretaceous protocardiids, Isle of Wight, Wiltshire, Devon, **17,** 165 (*407*). Middle Jurassic euryhaline oyster, **19,** 79 (*264*). Ecology of late Jurassic *Hiatella*, Lincolnshire, **23,** 769 (*302*). Jurassic anomiid(?), Oxfordshire, **25,** 897 (*214*).

BRACHIOPODA

Growth and microstructure of Jurassic thecideacean *Moorellina*, **13,** 76 (*27*). Variation in cardinalia of Silurian *Ptychopleurella*, Shropshire, **13,** 297 (*38*). Morphology and microstructure of Middle Jurassic *Zellania*, **13,** 606 (*28*). Lower Carboniferous endopunctate rhynchonellid, Derbyshire, Staffordshire, Yorkshire, **14,** 95 (*83*). Lower Silurian Stropheodontidae, Welsh Borderland, **14,** 303 (*39*). New Middle Jurassic micromorphic rhychonellide, Gloucestershire, **14,** 696 (*29*). Loop development in Middle Jurassic *Zeilleria*, Cotswolds, **15,** 450 (*30*). Middle Devonian *Bifida* and *Kayseria*, Devonshire, **16,** 117 (*135*). Silurian communities, Welsh Borderland, **17,** 779 (*92*). Lower Carboniferous fauna, Staffordshire, **17,** 811 (*85*). Terebratulide affinity of Middle Jurassic *Spirifera minima*, Gloucestershire, **18,** 879 (*32*). Lower Cretaceous terebratulaceans, Bedfordshire, **21,** 411 (*139*). Phenetic strategy model for Ordovician–Silurian dalmanellids, Welsh Borderland, **21,** 535 (*270*). Lower Cretaceous thecideidines, Oxfordshire, **21,** 555 (*33*). Lower Silurian acrotretaceans, Welsh Borderland, **22,** 93 (*116*). Anomalous occurrences of Ordovician–Silurian *Schizocrania*, Shropshire, **23,** 707 (*340*).

BRYOZOA

Exceptional preservation in Middle Jurassic cyclostomes, Northamptonshire, **16,** 219 (*574*). Multilamellar growth in Middle Jurassic cyclostomes, Wiltshire, Gloucestershire, Surrey, **19,** 293 (*539*). Middle Jurassic *Terebellaria*, Somerset, Dorset, Wiltshire, **21,** 357 (*540*). New Jurassic species, Wiltshire and Gloucestershire, **23,** 699 (*541*). Jurassic Portland Beds fauna, Wiltshire and Dorset, **24,** 863 (*542*). Palaeobiology of Pliocene cyclostomes, Suffolk, **25,** 529 (*35*).

CONODONTOPHORIDA

Givetian–Frasnian faunas, Cornwall, **13,** 335 (*323*). Lower Carboniferous fauna, Devonshire, **15,** 550 (*372*). Lower Carboniferous faunas, eastern Mendips, **16,** 477 (*91*). Lower Carboniferous faunas, Devonshire, **17,** 371 (*373*). Middle–Upper Devonian biostratigraphy, Devonshire, **21,** 907 (*400*). Upper Carboniferous coprolitic assemblages, Staffordshire, **24,** 437 (*252*). Lower Carboniferous faunas, Cumbria, **25,** 145 (*253*). Derived and indigenous elements in upper Permian strata, Nottinghamshire and Yorkshire, **25,** 845 (*527*).

CRINOIDEA

Lower Silurian *Promelocrinus*, West Midlands, **19,** 651 (*82*).

CRUSTACEA

Middle–Upper Cambrian bradoriids, Warwickshire, **21,** 245 (*475*).

DECAPODA

New Eocene crabs, Hampshire Basin, **24,** 733 (*444*).

England (*cont.*):

ECHINOIDEA

Upper Cretaceous sympatric species of *Micraster*, Kent and Norfolk, **19,** 689 (*523*). Upper Cretaceous *Micraster* and *Epiaster*, **20,** 805 (*524*). Palaeobiology of Upper Cretaceous irregular genera, **25,** 11 (*216*). Tooth structure of Jurassic pyasteroid *Plesiechinus*, Gloucestershire, **25,** 891 (*507*).

FORAMINIFERA

Surface textures of Tertiary calcareous tests, Hampshire Basin, **13,** 184 (*393*). Unusual new Upper Cretaceous agglutinating form, Kent, **16,** 637 (*3*). Evolution of Lower Cretaceous *Arenobulimina*, *Gavelinella* and *Hadbergella*, **20,** 503 (*443*). Upper Cretaceous *Gavelinella*, **24,** 391 (*170*).

FUNGI

Fungal spores of early Tertiary *Ctenosporites*, Hampshire Basin, **21,** 717 (*508*). Eocene–Oligocene trichothyriaceous fungi, Hampshire Basin, **23,** 205 (*509*).

INSECTA

Upper Carboniferous palaeodictyopteran nymphs, Lancashire and Yorkshire, **15,** 662 (*598*).

MALACOSTRACA

Cuticle ultrastructure of Middle Jurassic lobster *Eryma*, Oxfordshire, **14,** 201 (*397*).

MAMMALIA

Middle Jurassic mammal bed, Oxfordshire, **22,** 135 (*209*).

MEROSTOMATA

New Upper Carboniferous xiphosurid, Somerset, **15,** 569 (*14*).

MICROPLANKTON

Lower Ordovician acritarchs *Priscogalea* and *Cymatiogalea*, Shropshire, **17,** 41 (*446*). Upper Triassic–Lower Jurassic dinoflagellate *Rhaetogonyaulax*, **18,** 847 (*243*). Distribution of Palaeogene dinoflagellate *Wetzeliella*, London and Hampshire basins, **19,** 591 (*137*). Middle Jurassic dinoflagellates and acritarchs, Dorset, Oxfordshire, Somerset, **23,** 151 (*196*). Eocene–Oligocene dinoflagellate cysts, Isle of Wight, **23,** 475 (*338*). Reworked acritarchs in type Ordovician rocks, Shropshire, **25,** 119 (*566*).

OSTRACODA

Upper Silurian faunas, Westmorland, **14,** 595 (*498*). Lower Jurassic fauna, Yorkshire, **14,** 642 (*346*). New Lower Jurassic genera *Wicherella* and *Gramannella*, **15,** 187 (*347*). Oligocene faunas, Isle of Wight, **15,** 267 (*300*). Lower Jurassic faunas, **17,** 599 (*348*). Upper Jurassic freshwater fauna, Dorset, **18,** 419 (*37*). Eocene assemblages and depositional environments, Hampshire Basin, **20,** 405 (*301*). Middle Pleistocene freshwater assemblages, Norfolk, **22,** 293 (*154*).

PALAEOECOLOGY

Slumping in Devonian Goniatite Bed, Devonshire, **15,** 430 (*568*). Upper Jurassic palaeoenvironments, Dorset, **16,** 261 (*79*). Limpet grazing on Cretaceous algal-bored ammonites, Kent, **25,** 361 (*4*).

PISCES

Cretaceous otoliths, **16,** 293 (*521*). New Eocene scyliorhynid shark teeth, Essex, **20,** 195 (*96*). Dentition of Middle Jurassic *Brachymylus*, Northamptonshire, **20,** 589 (*576*). New Devonian articulated thelodont, Herefordshire, **25,** 879 (*567*).

PLANTAE

Eocene *Platanus* wood, Suffolk, Essex, Kent, **15,** 496 (*73*). Upper Jurassic gymnospermous wood, Norfolk, **15,** 655 (*144*). *In situ* Upper Eocene coniferous trees, Hampshire Basin, **16,** 205 (*207*). Middle Jurassic *Williamsoniella* and its pollen, Yorkshire, **17,** 125 (*245*). Lower Devonian flora, Shropshire, **17,** 311 (*169*). Leaf anatomy of Lower Cretaceous fusainized *Weichselia*, Isle of Wight, **17,** 587 (*9*). Upper Jurassic land plants and Charales, Dorset, **18,** 419 (*37*). Lower Cretaceous debris beds, Sussex, Dorset, Isle of Wight, **19,** 437 (*399*). Upper Carboniferous plant debris in coprolites, Yorkshire, **20,** 59 (*487*). Evolution of Eocene–Oligocene charophyte floras, Isle of Wight, **20,** 143 (*194*). Lower Cretaceous Cheirolepidiaceae conifers, Sussex, **20,** 715 (*579*). Early Devonian flora, Oxfordshire, **21,** 687 (*99*). Lower Cretaceous *Classopollis*-bearing cone associated with *Pseudofrenelopsis*, Isle of Wight, **21,** 847 (*13*). Upper Jurassic araucarian cone, Dorset, **23,** 657 (*522*). Petrified Upper Carboniferous fern sporangium, Lancashire, **24,** 483 (*222*). Anatomy and palaeoecology of Cretaceous *Pseudofrenelopsis* and associated conifers, Isle of Wight, **24,** 759 (*11*).

POLLEN and SPORES

Lower Cretaceous palynological assemblages in correlation, **16,** 1 (*47*). Lower Cretaceous soil beds, Sussex and Surrey, **16,** 399 (*48*). Lower Cretaceous correlation, Dorset and Surrey, **16,** 567 (*267*). Middle Jurassic *Williamsoniella* and compression of spherical pollen grains, Yorkshire, **17,** 125 (*245*). Lower Devonian assemblages, Shropshire, **17,** 311 (*169*). Megaspores and massulae of Oligocene *Azolla*, Isle of Wight, **18,** 483 (*206*). Lower–Upper Cretaceous angiosperm assemblages, Dorset and Hampshire, **18,** 775 (*330*). Upper Palaeocene salviniacean massulae, Kent, **19,** 173 (*365*). Lower Cretaceous plant debris beds, Sussex, Dorset, Isle of Wight, **19,** 437 (*399*). Early Devonian *in situ* spores, Oxfordshire, **21,** 687 (*99*). Lower Cretaceous *Classopollis*-bearing cone associated with *Pseudofrenelopsis*, Isle of Wight, **21,** 847 (*13*). Lower Cretaceous earliest angiosperm pollen, **22,** 513 (*268*). New Eocene multiple-floated *Azolla*, Isle of Wight, **23,** 213 (*124*).

PROBLEMATICA

New Lower Cretaceous possible alga, Berkshire, **15,** 501 (*176*). Lower Cambrian lapworthellids, Shropshire, **16,** 139 (*369*).

REPTILIA

Upper Cretaceous chelonians, Cambridgeshire, **13,** 355 (*119*). New Lower Eocene trionychid turtle, Sussex, **13,** 503 (*383*). Middle Jurassic megalosaurids, Dorset, **17,** 325 (*571*). Lower Permian pelycosaurs, Warwickshire, **17,** 541 (*418*). New Lower Eocene trionychid turtle, Kent, **17,** 901 (*572*). Cranial morphology of new Lower Cretaceous turtle, Dorset, **18,** 25 (*187*). Jurassic–Cretaceous hypsilophodontid dinosaurs, **18,** 741 (*217*). New Lower Cretaceous turtle skull, Dorset, and early dichotomies of cryptodires, **19,** 317 (*188*). Middle Jurassic dinosaur, Oxfordshire, **19,** 587 (*218*). Lower Cretaceous crocodilian *Bernissartia*, Isle of Wight, **22,** 905 (*88*). Upper Jurassic ornithischian dinosaur *Camptosaurus*, Oxfordshire, **23,** 411 (*219*). Lower Jurassic plesiosaur embryos reinterpreted as shrimp burrows, Yorkshire, **25,** 351 (*556*). New Upper Triassic rhynchocephalian, Gloucestershire, **25,** 709 (*208*).

SCAPHOPODA
New Middle Jurassic species, Buckinghamshire, **18,** 377 (*408*).

STRATIGRAPHY
Lower Silurian, Welsh Borderland, **17,** 745 (*40*). Upper Jurassic faunas and stratigraphy, Dorset, **21,** 469 (*134*).

STROMATOLITES
Upper Triassic algal tuft structures, south-west England, **24,** 655 (*374*).

TRACE FOSSILS
New Upper Carboniferous xiphosurid trails, **13,** 188 (*239*). Middle Jurassic *Thalassinoides* burrow containing crustacean, Oxfordshire, **14,** 589 (*493*). Upper Carboniferous coprolites containing plant debris, Yorkshire, **20,** 59 (*487*). Invertebrate traces from Cheshire compared with south German forms, **24,** 555 (*438*). Lower Jurassic plesiosaur embryos reinterpreted as shrimp burrows, Yorkshire, **25,** 351 (*556*). Limpet grazing on Lower Cretaceous algal-bored ammonites, Kent, **25,** 361 (*4*).

TRILOBITA
New Lower Ordovician genus *Anebolithus*, Shropshire, **13,** 677 (*266*). Lower Carboniferous fauna, Somerset, **16,** 551 (*233*). Middle Ordovician faunas, south Cornwall, **17,** 71 (*477*). Affinities of upper Silurian *Scharyia*, Herefordshire and Shropshire, **17,** 685 (*402*). New lower Silurian proetacean, West Midlands, **18,** 809 (*404*). Upper Ordovician *Phillipsinella*, Cumbria, **19,** 699 (*87*). Silurian *Encrinurus*, West Midlands and Welsh Borderland, **20,** 847 (*563*). Synonymy of Lower Carboniferous *Namuropyge* and *Coignouina*, Derbyshire, **20,** 917 (*379*). Middle–Upper Cambrian transition faunas, Warwickshire, **21,** 245 (*475*). Upper Ordovician fauna, Cumbria, **22,** 53 (*357*). Evolution of lower Silurian *Tapinocalymene*, Welsh Borderland, **23,** 783 (*503*).

France

ALGAE
Reproductive structures in new Miocene solenoporacean, Brittany, **16,** 223 (*178*). Middle Jurassic *Stichoporella*, Paris Basin, **22,** 407 (*183*).

AMMONOIDEA
Upper Cretaceous *Acanthoceras*, Rouen, **13,** 462 (*308*). Lower Cretaceous *Lyticoceras* and its synonym *Endemoceras*, **18,** 607 (*603*). Lectotype of Middle Jurassic *Cadomites*, Normandy, **18,** 871 (*590*). Upper Cretaceous *Stoliczkaia*, Sarthe, **21,** 393 (*605*). Type Upper Cretaceous vascoceratids, Touraine, **22,** 665 (*314*). Type Turonian *Romaniceras*, **23,** 325 (*317*). Upper Cretaceous collignoniceratids, **23,** 557 (*318*). Upper Cretaceous faunas, Anjou and Vendée, **24,** 25 (*310*). Type Turonian Desmocerataceae, Touraine, **24,** 493 (*316*).

BELEMNOIDEA
Palaeobiology of Upper Cretaceous faunas, Paris Basin, **23,** 889 (*282*). Lower Cretaceous diplobelinids, Paris Basin, **24,** 115 (*285*).

BIVALVIA
Dentition and musculature of Middle Ordovician palaeotaxodontids and palaeoheterodontids, Brittany, **13,** 623 (*69*). Functional morphology of Ordovician palaeotaxodont hinges, Brittany, **14,** 242 (*68*). New Lower–Middle Jurassic genus ancestral to *Globocardium*, Calvados, **17,** 165 (*407*). Middle–Upper Jurassic anomiid?, Normandy, **25,** 897 (*214*).

BRYOZOA
Symbiosis between Middle Jurassic ectoprocts, gastropods and crabs, Calvados, **16,** 563 (*412*). Multilamellar growth in Middle Jurassic cyclostomes, Normandy, **19,** 293 (*539*). Middle Jurassic *Terebellaria*, Normandy, **21,** 357 (*540*).

DECAPODA
Symbiosis between Middle Jurassic ectoprocts, gastropods and crabs, Calvados, **16,** 563 (*412*).

FORAMINIFERA
Evolution of Lower Cretaceous *Arenobulimina*, *Gavelinella* and *Hedbergella*, **20,** 503 (*443*). Upper Cretaceous *Gavelinella*, **24,** 391 (*170*).

GASTROPODA
Feeding habits of Eocene predatory forms, Paris Basin, **13,** 254 (*534*). Symbiosis with Middle Jurassic ectoprocts and crabs, Calvados, **16,** 563 (*412*).

MAMMALIA
Miocene horse *Hipparion*, Mt. Léberon, **23,** 617 (*350*).

MICROPLANKTON
Lower Cretaceous dinoflagellate cysts, Vaucluse, **17,** 623 (*153*).

OSTRACODA
Oligocene faunas, Paris Basin, **15,** 267 (*300*).

PALAEOECOLOGY
Middle Jurassic sponge reefs, Normandy, **24,** 1 (*411*).

PLANTAE
Upper Triassic–Lower Jurassic flora, Manche, **13,** 433 (*390*).

POLLEN and SPORES
Lower–Upper Cretaceous angiosperm assemblages, Normandy and Sarthe, **18,** 775 (*330*).

PORIFERA
Ecology of Middle Jurassic reefs, Normandy, **24,** 1 (*411*).

REEFS
Ecology of Middle Jurassic sponge reefs, Normandy, **24,** 1 (*411*).

REPTILIA
Upper Cretaceous chelonian, Grenoble, **13,** 355 (*119*).

TRILOBITA
Ordovician *Eoharpes*, Brittany, **25,** 623 (*468*).

Germany (F.G.R.)

AMMONOIDEA
Preservational history of Triassic ceratite shells, **14,** 16 (*492*). Upper Cretaceous fauna, Rhenish Massif, **15,** 445 (*238*). Lower Cretaceous *Lyticoceras* and its synonym *Endemoceras*, **18,** 607 (*603*). Jaws of Lower Jurassic *Dactylioceras*, Reichenswand, **22,** 265 (*335*). Lower Cretaceous faunas of Tethyan ancestry, **24,** 251 (*303*).

AMPHIBIA
Replacement name for Triassic labyrinthodont *Parotosaurus*, Bernburg, **19,** 415 (*420*).

BRACHIOPODA
Middle Devonian *Bifida* and *Kayseria*, Eifel region, **16,** 117 (*135*). Shell structure of Devonian retziid *Plectospira*, **25,** 857 (*53*).

FORAMINIFERA
Evolution of Lower Cretaceous *Arenobulimina*, *Gavelinella* and *Hedbergella*, **20,** 503 (*443*).

MICROPLANKTON
Distribution of Palaeogene dinoflagellate *Wetzeliella*, **19,** 591 (*137*).

NAUTILOIDEA
Siphuncular structures in Middle Devonian *Archiacoceras*, Eifel region, **22,** 747 (*145*).

PISCES
Upper Jurassic selachian *Protospinax*, Bavaria, **19,** 733 (*360*).

REPTILIA
Osteology of Upper Jurassic lizard *Ardeosaurus*, Solnhofen, Bavaria, **25,** 461 (*367*).

TRACE FOSSILS
Invertebrate traces compared with English forms, **24,** 555 (*438*).

Ghana

PLANTAE
New Lower Carboniferous lycopods, Essipon, **14,** 357 (*375*). Non-vascular Middle Devonian land flora, Komenda, **17,** 925 (*100*).

Greenland

BIVALVIA
Upper Jurassic-Lower Cretaceous buchiids, **25,** 727 (*526*).

CONODONTOPHORIDA
Fused cluster of Upper Ordovician coniform elements, Washington Land, **25,** 425 (*6*).

TRILOBITA
New Silurian fauna, **15,** 336 (*331*).

India

CRINOIDEA
Silurian *Stephanocrinus*, Kashmir, **14,** 262 (*231*).

FORAMINIFERA
Middle Eocene *Nummulites*, Kutch [Cutch], **24,** 803 (*479*).

MAMMALIA
Neogene rodents, Siwalik Hills and Salt Range, **15,** 238 (*58*). New Eocene cetacean species, Kutch, **15,** 490 (*478*).

OSTRACODA
Middle Jurassic freshwater fauna, Pranhita-Godavari Valley, **18,** 207 (*226*). New Eocene trachyleberid genus, Rajasthan and Kutch, **24,** 877 (*502*).

PISCES
New Lower Jurassic holosteans, Pranhita Godavari Valley, **16,** 149 (*281*).

REPTILIA
New Triassic dicynodont, Pranhita Godavari Valley, **13,** 132 (*107*). Primitive late Triassic parasuchid, Pranhita-Godavari Valley, **21,** 83 (*103*).

Indian Ocean

ALGAE
Girvanella-calcified sheath of Recent *Plectonema*, Aldabra, **20,** 33 (*455*).

FORAMINIFERA
Oligocene-Miocene biostratigraphy, Christmas Island, **17,** 475 (*1*).

REEFS
Pleistocene molluscan assemblages and faunal response to habitat instability, Aldabra, **21,** 1 (*536*).

Indonesia

ANTHOZOA
Structure and composition of upper Permian rugosans, Timor, **21,** 321 (*513*).

Iran

ALGAE
New Palaeocene dasycladacean, Kurdistan, **21,** 687 (*182*).

Iraq

ALGAE
Permian and Cretaceous Codiaceae, **13,** 327 (*172*). New Palaeocene dasycladacean, Kurdistan, **21,** 687 (*182*).

Ireland

ALGAE
Ecology of Recent free-living coralline forms, Connemara, **19,** 365 (*62*). Recent coralline gravels, Co. Galway, **22,** 449 (*63*).

AMPHIBIA
Upper Carboniferous temnospondyl *Dendrerpeton*, Co. Kilkenny, **23,** 125 (*381*).

ANTHOZOA
Variation in Lower Carboniferous *Caninia*, Co. Sligo, **13,** 52 (*158*). Distribution and growth of Lower Carboniferous caninioids, Co. Sligo and Co. Donegal, **13,** 191 (*263*).

BIVALVIA
Late Ordovician fauna, Co. Tyrone, **25,** 43 (*565*).

BRACHIOPODA

Lower Carboniferous endopunctate rhynchonellid, Co. Cork, **14,** 95 (*83*). Endemic lower Silurian species, Co. Kerry, **19,** 615 (*42*). Micro-ornamentation of Lower Carboniferous spiriferides, Co. Fermanagh, **19,** 767 (*84*).

BRYOZOA

Lower Carboniferous *Polypora* with cheilostomatous features, Co. Fermanagh, **14,** 178 (*530*). Early growth in Lower Carboniferous rhabdomesoids, Co. Wexford, **17,** 149 (*531*).

CONODONTOPHORIDA

Lower Carboniferous faunas, south-west Ireland, **16,** 335 (*371*).

PALAEOGEOGRAPHY

Implications of lower Silurian shelly faunas, Co. Tipperary and Co. Clare, **18,** 343 (*586*).

PORIFERA

Middle Cambrian *Protospongia*, Co. Mayo, **16,** 231 (*476*).

TRILOBITA

Lower Carboniferous fauna, Co. Dublin, **16,** 391 (*232*). New Lower Ordovician pelagic genus, Co. Galway, **17,** 111 (*203*). Upper Ordovician *Celtencrinurus* and *Cryptolithus*, Co. Tyrone, **21,** 455 (*564*).

Italy

ALGAE

Nature of *Aciculella*, South Tirol, **14,** 629 (*174*).

ANTHOZOA

Structure and composition of upper Triassic scleractinians, Dolomiti, **21,** 321 (*513*).

Jamaica

ALGAE

New Pliocene species of *Neomeris*, **14,** 623 (*445*).

Japan

AMMONOIDEA

Upper Cretaceous assemblages in *Scaphites* facies, Hokkaido, **22,** 609 (*529*).

BIVALVIA

Bizarre new Permian myalinid, Akasaka, **18,** 315 (*474*).

GASTROPODA

Mode of life of giant Upper Cretaceous capulid, **23,** 689 (*248*).

PALAEOECOLOGY

Mode of life of giant Upper Cretaceous capulid gastropod, **23,** 689 (*248*).

Jordan

FORAMINIFERA

Late Cretaceous-Palaeocene-early Eocene faunas and biostratigraphy, **19,** 517 (*215*).

Kenya

ANTHOZOA

Pleistocene reef succession and diversity, Kenya coast, **23,** 1 (*141*). Ecological stratification in Pleistocene reefs, Kenya coast, **24,** 609 (*142*).

MAMMALIA

New Upper Miocene proboscidean, Baringo District, **17,** 699 (*359*).

OSTRACODA

New sub-Recent *Hemicypris*, Lake Rudolf, **13,** 289 (*43*). Fossil and living *Hemicypris*, Lake Rudolf, **15,** 184 (*44*).

REEFS

Succession and diversity in Pleistocene coral reefs, Kenya coast, **23,** 1 (*141*). Ecological stratification in Pleistocene coral reefs, Kenya coast, **24,** 609 (*142*).

REPTILIA

New early Miocene crocodiles, Rusinga Island, **21,** 857 (*544*).

Lesotho

REPTILIA

Upper Triassic ornithischian dinosaur, Likhoele Mountain and Fort Hartley-Cutting Camp,**13,** 414 (*554*). Post-cranial skeleton of Triassic ornithischian dinosaur *Fabrosaurus*, Likhoele Mountain, **15,** 29 (*555*).

Libya

DECAPODA

New Middle Eocene carpiliid crab, **16,** 283 (*120*).

Malaysia

BIVALVIA

Bizarre new Permian myalinid, Perak, **18,** 315 (*474*).

CONODONTOPHORIDA

Upper Carboniferous faunas, Pahang, **23,** 297 (*376*).

Mauretania

BRACHIOPODA

Silurian *Clarkeia* fauna, **15,** 623 (*115*).

TRILOBITA

New Middle Devonian *Phacops*, Tindouf Basin, **17,** 349 (*90*).

Mongolia

REPTILIA

Juveniles of the Cretaceous ornithischian dinosaur *Psittacosaurus*, **25,** 89 (*130*).

Morocco

BRACHIOPODA

Lower Cretaceous terebratulids and biogeography, **23,** 515 (*378*).

TRILOBITA

New Middle Devonian *Phacops*, Tindouf Basin, **17,** 349 (*90*).

Netherlands

ECHINOIDEA
Lower Palaeocene salenioids, Maastricht area, **25**, 265 (*220*).

FORAMINIFERA
Evolution of Lower Cretaceous *Arenobulimina*, *Gavelinella* and *Hedbergella*, **20**, 503 (*443*).

New Zealand

BIVALVIA
Functional morphology of Devonian palaeotaxodont hinges, **14**, 242 (*68*).

DECAPODA
New Miocene spider-crab, Canterbury, **17**, 869 (*287*). Early Miocene *in situ* hermit crab, Southland, **23**, 471 (*273*).

ECHINOIDEA
Tertiary holasteroid faunas, **21**, 791 (*205*).

GRAPTOLITHINA
Taxonomy and evolution of Ordovician *Isograptus*, north-west Nelson, **16**, 45 (*132*).

TRILOBITA
Ordovician trinucleid *Incaia*, Paturau River, **13**, 677 (*266*).

Nigeria

DECAPODA
New Upper Cretaceous retroplumid, Abakaliki, Benue-Plateau and Enugu, **18**, 823 (*121*).

FORAMINIFERA
Upper Cretaceous arenaceous faunas, Iullemmeden Basin, **22**, 947 (*431*).

REPTILIA
Lower Cretaceous giant mesosuchian crocodile *Sarcosuchus*, Tegama basin, **20**, 203 (*89*).

North Sea

MICROPLANKTON
New Lower Cretaceous dinocysts, **22**, 427 (*152*).

Norway

AMMONOIDEA
Upper Jurassic–Lower Cretaceous faunas, Andøya, **21**, 31 (*56*).

BIVALVIA
Lower Cretaceous buchias, Andøya, **21**, 31 (*56*).

BRACHIOPODA
Lower Silurian pentamerids *Borealis* and *Pentamerus*, Oslo Region, **24**, 537 (*384*). Latest Ordovician fauna, Oslo–Asker, **25**, 755 (*117*).

CYSTOIDEA
Ordovician Hemicosmitidae, Oslo Region, **22**, 363 (*61*).

FORAMINIFERA
Upper Jurassic–Lower Cretaceous assemblages, Andøya, **22**, 413 (*345*).

MICROPLANKTON
Upper Jurassic–Lower Cretaceous dinocysts, Andøya, **21**, 31 (*56*).

PALAEOECOLOGY
Latest Ordovician regressive sequence, Oslo–Asker, **25**, 783 (*72*).

POLLEN and SPORES
Middle Jurassic assemblages, Andøya, **21**, 31 (*56*).

PROBLEMATICA
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